Impacts of climate change and fisheries on the Celtic Sea ecosystem

Valentina Lauria

A thesis submitted to Plymouth University

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Science and Technology

Faculty of Marine Science and Engineering

In collaboration with Natural England, Sir Alister Hardy Foundation for Ocean Science and the Centre for Environment, Fisheries and Aquaculture Science

April 2012

Abstract

Impacts of climate change and fisheries on the Celtic Sea ecosystem

Valentina Lauria

Climate change and fisheries have affected marine environments worldwide leading to impacts on ecosystem structure and functioning. However there is clear evidence of spatial variability in the response of these impacts both within and among marine ecosystems. Although several studies have tried to explain the effect of these impacts on marine food webs, it is unclear how they interact, and how they may affect marine ecosystems remains an important unanswered question. This suggests the urgent need for multiple-trophic level and ecosystem-based management approaches to account for both fisheries and climate change impacts at ocean basins across the globe. Marine apex predators, such as seabirds, are vulnerable to the effects of both climate and fishing impacts, and can be used as reliable and sensitive bio-indicators of the status of the marine ecosystem.

The Celtic Sea ecosystem is a productive shelf region in the Northeast Atlantic. It is characterized by high fish and invertebrate biodiversity. In addition, internationally important numbers of seabirds, such as Northern gannet *Morus bassanus* (L.), Manx shearwater *Puffinus puffinus* (B.), Common guillemot *Uria aalge* (P.) and Black-legged kittiwake *Rissa tridactyla* (L.), breed along the Celtic Sea coasts. In recent years, fisheries from across Europe have intensively exploited the Celtic Sea, leading to changes in stock structure. Moreover, the increase in annual average Sea Surface Temperature by 0.67 ^{o}C over the past two decades has altered the composition of plankton communities. These impacts, independently and in tandem, are likely to have had dramatic effects upon the

Celtic Sea food web emphasizing the need to enhance our understanding of this important marine ecosystem.

In this thesis the effects of climate change and fisheries on the Celtic Sea pelagic food web are evaluated, in particular focussing on the response of seabird populations. This is in part because of recent declines in the breeding success of many seabird colonies in the northeast Atlantic, particularly around the North Sea. Long-term data across four trophic levels (phytoplankton, zooplankton, mid-trophic level fish and seabirds) and different modelling approaches are used to determine factors influencing seabird productivity at different geographical scales. First, I review the direct and indirect effects of climate change and fisheries upon marine ecosystems, as well as their impacts upon marine birds. Second, I use data collected during 1986-2007 from a single seabird colony, across four trophic levels, to investigate long-term direct and indirect climate effects. The results suggest only a weak climate signal in the Celtic Sea, and this is only evident between mid-trophic level fish and certain species of seabird. Third, a similar multi-trophic level approach across three nearby regions in the southwest UK (Irish Sea, Celtic Sea, and English Channel) reveal no evidence of a bottom-up signal during the period 1991-2007. These findings are in contrast with the nearby North Sea region, where a strong bottom-up effect was found to affect seabird populations, highlighting the importance of regional-based studies across multiple trophic levels. Finally, to provide a more complete picture of the Celtic Sea, and how it might respond to changes in fisheries management and climatic variation, I use the complex tropho-dynamic ecosystem model Ecopath with Ecosim. The main focus is on how seabird biomass changes in response to the application of different fisheries regimes likely to be implemented under forthcoming reforms to the Common Fisheries Policy (e.g. the application of quotas and discard bans), as well as future climate change scenarios, in order

to provide guideline support for resource management and seabird conservation in the Celtic Sea. The results suggest that some seabird guilds (gulls and some other scavengers) may be negatively affected by a reduction in discards, while other species (offshore divers) will benefit from a decrease in the fishing of pelagic fish species. Climate change is likely to have a negative impact across all trophic levels with a strong negative impact upon seabird populations. Therefore seabirds are likely to show species-specific responses to both climate variation (bottom-up effect) and changes in fishing practices, in particular our findings suggest that for some species climate may outweigh the fisheries impacts even when fisheries pressure is reduced by 50%. In summary, this study suggests that despite the generally negative impact of climate described for some regions in the Northeast Atlantic, the Celtic Sea ecosystem seems to be more resilient. However, both climate and fisheries and the interactions between these factors should be taken into account in the formulation of future management plans for the Celtic Sea ecosystem. The use of multiple-trophic level and ecosystem-based approaches over multiple spatial and temporal scales has helped to elucidate possible trophic mechanisms that are the response to future fishing and climate impacts in the Celtic Sea. The results of this study could have implications for both management plans and conservation policy.

Table of contents

List of figures and tables

CHAPTER 2

WNAO: winter North Atlantic Oscillation index; SNAO: spring North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; 2lag-SSST: 2 years lagged spring Sea Surface Temperature; her 0-g: herring 0-group; her-1g: herring 1-group; Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented.

Table 2.4 Impact of climate variability across multiple trophic levels in the North Atlantic. SST: Sea Surface Temperature; NAO: North Atlantic Oscillation index.

CHAPTER 3

Figure 3.1 (a) Map of the study area, including frontal systems (adapted from OSPAR, 2004). The locations of kittiwake (*Rissa tridactyla*) colonies investigated in this study are also presented; 1: Great Ormes Head (53° 20N, 3° 51W), 2: Bardsey Island (52° 72N, 4° 77′W), 3: Skomer Island (51º 40N, 05º 15W), 4: Elegug Stacks (51º 60N, 04º 98W), 5: Dunmore East (51º 15N, 06º 99W), 6: Ram Head (51º 15N, 07º 70W), 7: Durlston Head (50º 54N, 02º 02W). (b) Map of the study area, showing the locations of all CPR samples for the three regions from March to June. In blues samples used for the Irish Sea (52ºN-55º, 7ºE-2ºW) spanning from 1991-2007, in green samples used for the Celtic Sea (50ºN-52º, 10ºE-5ºW) spanning from 1991-2007, in red sample used for the English Channel (49ºN-51º, 10ºE-1ºW) spanning from 1991-2004.

Figure 3.2 Variables used for the models construction for each region: Sea Surface Temperature (ºC) (a-c); Diatom abundance (d-f); copepods biomass (mg wet weight) (g-i); fish larval abundance (j-l); Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size) (m-p). The line indicates when temporal trends are present. Note the scales differ.

Table 3.1 Response variables and predictors used for the multiple regression models. For each response variable the full model is also given. WSST: Winter Sea Surface Temperature; 1Lag-SST: 1 year lagged annual Sea Surface Temperature; Kittiwake BS:

Ecotrophic Efficiency express as fraction of the production of i that is consumed within the system, exported or harvested.

Figure 4.2 The Celtic Sea Ecopath model in terms of relative biomass (size of circles) and its major energy flows within Functional Groups (FGs). The horizontal axis of symmetry of each box is aligned with the trophic level of this box. The value of a trophic level is a fractional because it depends on the diet composition of this group and on the trophic levels of its preys (Christensen and Pauly, 1993). Note that TL for Seabird surface feeders and Gulls the values were under estimated by Ecopath (respectively 3.82 and 2.46).

Figure 4.3 The Mixed Trophic Impacts Analysis in the Celtic Sea ecosystem. Seabird (impacted groups) response to the increase (by 10%) of other groups (impacting groups) biomass in the system. Positive impacts are shown above the base line in black (above the line) and negative impacts below in grey (below the line).

Figure 4.4 Trophic niche overlap index for seabird groups in the Celtic Sea calculated from the proportions of used resources in the diet matrix. Only groups with the highest values are shown. The index assumes values between 0 (no overlap) and 1 (total overlap).

CHAPTER 5

Table 5.1 Seabird and pelagic fish functional groups (FGs) used in the Ecosim scenarios. Seabird functional groups are adapted from JNCC, 2008. FGs structure in the model has previously described in Chapter 4 and Appendix 3.

Figure 5.1 Simulated scenarios of changing fishery mortality (F) of pelagic fish and predicted effects on their relative biomass. The arrow refers to 2015 when the reform of Common Fishery Policy (CPF) will enter into force. (a) Application of Maximum Sustainable Yield (MSY): the largest yield (or catch) that can be taken from a species' stock over an indefinite period. (b) Simulation of no changes in fishery pattern over time. (c) Increase of F over time followed by no-take ban from 2025.

Figure 5.2 Response of seabird groups to direct effects of simulated changes in pelagic fish fishery mortality (F) as outlined in Figure 1. (a) Application of Maximum Sustainable

Yield (MSY). (b) Simulation of no changes in fishery pattern over time. (c) Increase of F over time followed by no-take ban from 2025. Seabird offshore-surface feeders includes: northern gannet, black-legged kittiwake and northern fulmar; Seabird offshore divers includes: common guillemot, Atlantic puffin and razorbill; Gulls includes: lesser black backed gull, herring gull, great black backed gull, and black headed gull.

Figure 5.3 Effects of cessation of discarding on seabird biomass in the Celtic Sea estimated from Ecosim model. (a) Seabird biomass change following a discard ban. (b) Seabird biomass change following a discard ban, but with model including increasing seabird foraging time. Biomass values for FGs were recorded at 2020.

Figure 5.4 Seabirds response to climate forcing on Primary Production (PP). (a) Only changes to PP are applied while fishery is kept at constant value. (b) Both climate and fishery are modified; in particular fishery effort is reduced of 50% from 2015.

APPENDIX 1

Figure A1.1 Herring and sprat landings (kg/km^2) from the Western and Celtic Sea Ground Fish Survey (WCGFS) (CEFAS). This trawl survey is designed to study the distribution, composition and abundance of all fish, commercial shellfish and cephalopod species in the Celtic Sea. Pearson's coefficient of correlation: 0.715, p value= 0.001.

Table A1.1 Correlation matrix (Pearson's coefficient) between covariates. Significance is indicate as follow: pvalue< 0.001 ***, pvalue,< 0.01**, pvalue<0.05* SNAO: spring North Atlantic Oscillation index; WNAO: winter North Atlantic Oscillation index; SSST: spring Sea Surface Temperature; WSST: winter Sea Surface Temperature; Small cop: small copepods (<2mm); Large cop: large copepods (>2mm); KittBS: black-legged kittiwake productivity; GuiBS: guillemot productivity; RazBS: razorbill productivity; PufBS: puffin productivity; Her 0-g: herring 0-group; Her-1g: herring 1-group; Large cop: large copepod; Small cop: small copepods; KittRt: black-legged kittiwake population growth rate; GuiRt: guillemot population growth rate; RazRt: razorbill population growth rate; PufRt: puffin population growth rate.

Table A1.2 Competing models for low trophic levels. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; Significant relationships are highlighted in **bold,** not significant variables included in the model are also presented.

Table A1.3 Competing models for mid trophic levels. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; 2lag-SSST: 2 years lagged spring Sea Surface Temperature; large cop: large copepods (>2mm); significant relationships are highlighted in **bold**, not significant variables included in the model are also presented.

Table A1.4 Competing models for apex predators. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; SNAO: spring North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; her 0-g: herring 0-group; her-1g: herring 1-group; Significant relationships are highlighted in **bold**, not significant variables included in the model are also presented.

APPENDIX 2

Table A2.1 Correlation matrix (Pearson's coefficient) between covariates for the Irish Sea. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Bard: black-legged kittiwake productivity at Bardsey colony; Kitt Great: black-legged kittiwake productivity at Great Ormes Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

Table A2.2 Correlation matrix (Pearson's coefficient) between covariates for the Celtic Sea. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. KittEleg: black-legged kittiwake productivity at Elegug Stacks colony; KittSkom: black-legged kittiwake productivity at Skomer colony; KittDumn: black-legged kittiwake productivity at Dunmore East colony; KittRam: black-legged kittiwake productivity at Ram Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

Table A2.3 Correlation matrix (Pearson's coefficient) between covariates for the English Channel. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Durl: black-legged kittiwake productivity at Durlston Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

Table A2.4 Correlation matrix (Pearson's coefficient) between covariates in different regions. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Bard: black-legged kittiwake productivity at Bardsey colony; Kitt Great: black-legged kittiwake productivity at Great Ormes Head colony; Kitt Eleg: black-legged kittiwake productivity at Elegug Stacks colony; Kitt Skom: black-legged kittiwake productivity at Skomer colony; Kitt Dumn: black-legged kittiwake productivity at Dunmore East colony; Kitt Ram: black-legged kittiwake productivity at Ram Head colonycolony Kitt Durl: black-legged kittiwake productivity at Durlston Head colony; Cop: copepods; Diat: diatoms; flarvae: fish larvae; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

Table A2.5 Competing models for the Irish Sea. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. 1lag-SST: 1 year lagged annual Sea Surface Temperature. Significant relationships are highlighted in **bold**; not significant variables included in the model are also presented.

Table A2.6 Competing models for the Celtic Sea. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient.

Significant relationships are highlighted in **bold**; not significant variables included in the model are also presented.

APPENDIX 3

Table A3.1 Life table for seabird species in the Ecopath model.

Table A3.2 Information of abundance, biomass, and residence time of seabird species in the Celtic Sea area.

Table A3.3 Food conversion efficiency values P/Q year $^{-1}$ for invertebrate groups.

Table A3.4 Data derived best estimates for input parameters, with sources summarised. P/B is the Production/biomass ratio over year and it is equivalent to the instantaneous rate of total mortality. Q/B is the Consumption/biomass ratio, where consumption represents the intake of food by a group over year.

Table A3.5 Diet matrix showing input values.

Table A3.6 Sensitivity of estimated EE or biomass of selected FGs of 50% change in input biomass or EE of other FGs. Only sensitivities > 30% are shown. FG: functional group; IP: input parameter; EP: Estimated parameter; EE express the fraction of the production that is used in the system.

APPENDIX 4

Figure A4.1 (a) Celtic Sea ecosystem response to a small increase in combined fishing effort. The bottom plot shows an increase in fishing effort from the baseline (1.0). The upper plot shows groups that are temporarily disturbed and their subsequent recovery. (b) Ecosystem response to cessation of fishing. Upper plot shows the system response.

Figure A4.2 Parameterised stock-recruitment curve for some fish species in the Celtic Sea model.

Figure A4.3 Effects on changes in the vulnerability parameter setting on the persistence of functional groups (a) v=1.4; (b) v=2; (c) v=3; (d) v=4; (e) v=20 (the latter is presented only to show the erratic model behaviour under high vulnerability value setting).

Figure A4.4 Celtic Sea model fit to time series data. Fish data were collected from ICES stock assessment, plankton data from the Continuous Plankton Recorder (SAHFOS), and seabird data from the national Seabird Monitoring Programme database (Joint Nature Conservation Committee, JNCC); more details are given in the material and methods section of the manuscript. Weights applied in the model fitting are also shown: (1) weight applied, (0) weight not applied for that group.

Table A4.1 Time series used in the model fitting.

Table A4.2 Group feeding parameters in Ecosim (values used in the fitted model).

Table A4.3 Correlation analyses (Pearson's coefficient) of environmental parameters and plankton groups were used to help select parameters for time series (1991-2005) fitting. Significant correlations are shown in bold. Significance is indicated as follow: p value <0.001 ***, p value <0.01**, p value <0.05*. WNAO: Winter North Atlantic Oscillation (average December-March); AMO: Atlantic Multidecadal Oscillation; PP: Phytoplankton Color Index; Zoopl: Zooplankton biomass; Euph: Euphausiids biomass; WSST: Winter Sea Surface Temperature (average December-March).

Table A4.4 Vulnerability matrix for the fitted Celtic Sea model.

Acknowledgements

The PhD is an adventure and journey of self-discovering where you learn that there are aspects of yourself of which you ignored the existence before…

During my journey I had the opportunity to work and interact with some special people which I would like to thank. Firstly I would like thank all my supervisors: Steve Votier, Martin Attrill, Andy Brown and Martin Edwards for their guidance, knowledge and encouragement during all this time. Huge thanks to my funders: Plymouth University and Natural England for this PhD studentship and in particular to Steve, Andy and Martin for searching and finding extra-funding when my studentship ran out!!

A big thank you to all the people that have helped me to collate all the data used in this work, in particular David Johns and Priscilla Licandro for the plankton data and advices; Georg H. Engelhard, and Jeroen van der Kooij for their help, suggestions and conversations on pelagic fish species, and the Joint Nature Conservation Committee for access to the Seabird Monitoring Programme database along with all the people which have collected the data.

Huge thanks to John Pinnegar and Steve Mackinson for their help, patience and time to answer all my questions on Ecopath and Ecosim!

Massive thanks to my two proof readers! Kate and Alex I really have no words to thank you for reading "heavy modelling stuff"… Kate you have been amazing, and Alex thanks for being able to ignore that football/rugby was on TV…

Finally, huge thank to all my *"Plymouth-friends"* for all the laughs, great moments and support during my life here especially all the times I was complaining about the weather, they are: Kate, Maria, Sam, and Jaime. Another huge thank to my *"Italian-Plymouth-friends"*: Elena and Giulio how I could forget such a great time. Massive thank to my *"Sicilian-friends"*: Titti, Paolo and Monica, thanks for always being there for me. To my brother Dario and the rest of the family, thank you. And finally to my Alex for being such an amazing person, and coping with me… we finally made it!!

Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without the prior agreement of the Graduate Committee. This study was financed with the aid of a studentship from the Plymouth University and Natural England. The work described in this thesis was conducted by the author, under the supervision of Dr. Stephen Votier, Prof. Martin Attrill, Dr. Andrew Brown and Dr. Martin Edwards. Regular scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes and several papers prepared for publication.

Presentations and Conferences Attended:

Lauria, V., Attrill, M. J., Edwards, M., Brown, A., & Votier, S.C., 2011.
Modelling the effect of climate change on apex predators in the Celtic Sea using a multi-trophic level approach.
Oral presentation, Seabird Group 11th International Conference, Plymouth, UK, 2-4th September 2011.

Lauria, V., Attrill, M. J., Edwards, M., Brown, A., & Votier, S.C., 2011.
The relative influence of climate change and fishing impact on long-term trends in North Atlantic fish biomass and seabird populations.
Invited Speaker, CCMAR Seminars, University of Algarve, Faro, Portugal, 19th May 2011.

Lauria, V., Attrill, M. J., Edwards, M., Brown, A., & Votier, S.C., 2011.
Modelling the bottom-up effect on the Celtic Sea pelagic food web using a multi-trophic level approach.
Poster, Sir Alister Hardy Foundation for Ocean Science, 40th Council Meeting, Plymouth, UK, 13-14 April 2011.

Lauria, V., Pinnegar, J.K., Mackinson, S., Attrill, M. J., Edwards, M., Brown, A., & Votier, S.C., 2010.
Modelling anthropogenic impacts on the Celtic Sea trophic food web using an ecosystem-based approach.
Oral Presentation, Italian Society of Ecology, Rome, Italy, 27-30th September 2010.

Lauria, V., Pinnegar, J.K., Mackinson, S., Attrill, M. J., Edwards, M., Brown, A., & Votier, S.C., 2010.

Modelling the effects of climate and fishing on seabirds: an application of Ecopath with Ecosim models.
Oral presentation, 1st World Seabird Conference, Victoria, Canada, September 7th-11th 2010.

Lauria, V., Pinnegar, J.K., Mackinson, S., Attrill, M. J., Edwards, M., Brown, A., Campbell, M.S., & Votier, S.C., 2010.
Effects of climate and fishing on apex main predators: Ecopath with Ecosim modelling the Celtic Sea ecosystem.
Oral presentation, Ocean Science Meeting, Portland, Oregon, USA, 22nd-26th February, 2010.

Workshops attended

Osmose - Objected Oriented Simulator of Marine Ecosystem workshop (15-16 June 2009, IFREMER-CNRS, Sete- France).

AMEMR - Advances in Marine Ecosystem Modelling Research workshop "Bringing the gap between lower and higher trophic levels" (10-12 February 2009, Plymouth).

Word count of main body of thesis: 28,341

Signed:

Date:

Chapter 1

General introduction

While each of the chapters presented in this thesis has been written as a separate piece of research, it is intended that in combination they provide a better understanding of the marine spatial and trophic ecology of seabirds under climate change and fisheries impacts, with particular focus on the Celtic Sea. In this general introduction the key themes and the rationale behind this project are established, before highlighting the main aims of each chapter.

1.1 MARINE ECOSYSTEM CHANGE

Marine ecosystems are constantly exposed to changes of a natural or anthropogenic origin. Natural changes may influence local weather patterns and climate variables, such as temperature, wind and currents, but are generally thought to occur over long time periods (Hurrell and Deser, 2010). In contrast, anthropogenically driven changes appear to happen rapidly and constitute the strongest impacts upon the marine environment because they increase the frequency of natural occurring changes (Corti et al., 1999), leading to dramatic changes in the marine ecosystem (Pachauri, 2007). For instance, carbon emissions are thought to be responsible for global warming trends that will increase sea surface temperatures (SSTs) by an average of 1.3-1.8°C by the mid-century (2046-2065; IPCC, 2007), and are also predicted to affect seawater chemistry by increasing ocean acidity (Raven et al., 2005; IPCC, 2007).

These changing conditions have already greatly affected the functioning and productivity of marine ecosystems, with impacts across all trophic levels (Cushing, 1982; Richardson and

Shoeman, 2004; Sandvik et al., 2008). Marine ecosystems are also significantly impacted by other human activities, such as pollution (Votier et al., 2005, 2008; Österblom et al., 2007), and fisheries (Pauly et al., 1998). Pollution inputs into the oceans increase nutrient levels which can lead to eutrophication, having drastic impacts upon marine biodiversity (Worm et al., 2002, 2006; Frank et al., 2005), in addition pollution can have profoundly negative impacts upon the marine environment increasing mortality via oil spills (Camphuysen et al., 2002), and the accumulation of plastics (Thompson et al., 2004).

Commercial fisheries represent one of the most pervasive impacts upon marine ecosystems and this pressure has increased over time (Pauly et al., 2005), with global impacts upon sustainability (Pauly et al., 2002), and transformations in the structure and functioning of marine food webs which is reflected in the reduction of mean trophic levels and the size of landings (Pauly et al., 1998; Pinnegar et al., 2002; Blanchard et al., 2005).

In marine pelagic ecosystems energy flows travel across trophic levels from phytoplankton (primary producers) through zooplankton and pelagic schooling fish, to apex predators such as marine mammals and seabirds (Jennings et al., 2001). Responses to environmental and anthropogenic perturbations vary substantially across species, taxonomic groups and trophic levels (Wootton, 1998).The effect of climate variation can influence the energy flow in the ecosystem by a mechanism known as “bottom-up control”, where the regulation of the trophic food web is determined by lower trophic levels in response to environmental changes (Ottersen et al. 2004a, Frederiksen et al. 2006). Conversely “top-down control” describes the situation where the control is exercised by one or several upper-level predators (i.e. seabirds, marine mammals) or human-induced impacts like fisheries (Österblom et al., 2007). Recently, considerable attention has been given to the mid-trophic (zooplankton-feeding) level in marine trophic webs, which tends to be occupied by a few

abundant species, usually pelagic schooling fish (Durant et al., 2009). These key species exert significant control over the energy flows through the ecosystem by channelling energy and nutrients from planktonic primary and secondary producers to top predators; in addition they often fluctuate greatly in abundance, leading to a wasp-waist control of the ecosystem (i.e. controlling both primary and secondary producers as well as predators) (Cury et al., 2000; Fauchald et al., 2011).

Marine food webs can be regulated by a dynamic control that can alternate between bottom-up and top-down influences depending upon climate variation, anthropogenic pollution and over exploitation of fish stocks (Hunt et al., 2002; Litzow and Ciannelli 2007; Cury et al., 2008). Understanding which mechanisms are involved in trophic relationships is not always easy, and quantifying the effects of natural or anthropogenic change on apex predators requires further advances in our understanding of complex marine systems. This is because physical processes and fisheries effects often confound each other, making it hard to accurately identify the effects of anthropogenic pressures, and to measure the effectiveness of management actions. For example, environmental variability and climate-forced changes may act to mask the effects that fisheries have on ecosystem processes; or depleted fish stocks may be more likely to collapse owing to environmental fluctuations or climate variability (Steele, 1998; Pauly et al., 2002). In addition, it is important to consider the role of spatial variability across oceanographic regions and how this can affect the response of marine ecosystems to human-induced change (Richardson and Shoeman, 2004; Beaugrand et al., 2009; McGinty et al., 2011). Marine ecosystems are not equally sensitive to climate change or fisheries impacts, and they are likely to respond to variations in different ways according to their own history and resilience. In the North Atlantic, studies have revealed the importance of thermal boundaries which define vulnerable regions where

a small increase in temperature causes abrupt ecosystem shifts across multiple-trophic levels (Beaugrand et al., 2008). These findings underline the strong need for regional ecosystem-based studies across the North Atlantic, in order to improve our understanding of marine systems and provide scientific support for biodiversity conservation management schemes.

1.2 THEORETICAL CONSIDERATIONS: SEABIRDS AS INDICATORS OF MARINE ECOSYSTEM CHANGE

Seabirds are typically apex predators in marine systems, and can be used as bio-indicators of environmental change (Montevecchi 1993; Furness and Camphuysen 1997; Piatt and Sydeman, 2007; Parsons et al., 2008; Durant et al., 2009). They are vulnerable to a diverse range of anthropogenic pressures such as pollution (Votier et al., 2005), climate change (Thomas et al., 2004; Gremillet and Boulinier, 2009), commercial fisheries (Lewison et al., 2004; Votier et al., 2004b), and marine renewables (i.e. offshore wind power) (Fox et al., 2006).

Seabirds respond to changes in the marine ecosystem such as food availability, and numerous parameters can be used to gain information about their condition across different time scales: on a short-term scale of days to weeks (e.g. clutch size, adult and chick parameters); over a period of months (e.g. chick growth and breeding parameters); and over years to decades (e.g. population parameters) (Einoder et al., 2009).

Seabird breeding biology can indicate short- and long-term changes in oceanographic conditions or changes in fish stock sizes over much larger areas than the immediate foraging grounds around the colony (Schreiber and Schreiber, 1984; Hunt and Schneider, 1987; Croxall et al., 1988; Montevecchi and Berutti, 1990; Kitaysky and Golubova, 2000).

Seabird populations have declined under conditions of reduced prey availability (Aebischer et al., 1990; Bost and Le Maho, 1993; Oro and Furness 2002; Wanless et al., 2007), and in some instances this has coincided with the activity of local industrial fisheries (Frederiksen et al., 2008a).

Monitoring seabird breeding numbers and productivity over decadal-scale periods is a valuable means of investigating environmental changes (Croxall, 2006; Montevecchi, 2007; Einoder, 2009). In recent years, extensive effort has gone into monitoring the reproductive performance of seabirds; the breeding season is the most energetically demanding period of the seabird life cycle, and a successful outcome is critically dependent upon the availability of high quality food (Wanless et al., 2005). In fact, under adverse environmental conditions, such as food shortages, top predators reduce their breeding effort in order to conserve energy and survive periods of resource scarcity, making a trade-off between current and future reproductive success (Drent and Daan, 1980; Cairns, 1987). In some regions of the North Atlantic, a strong negative effect of climate and fisheries were shown to be the cause of the decline of seabird productivity (Furness and Tasker, 2000; Frederiksen et al., 2004a; Poloczanska et al., 2004), however, very little is known about the implications of climate change and fisheries on seabird populations in other areas.

1.3 SEABIRDS-CLIMATE CHANGE EFFECTS

In the North Atlantic relatively few studies have been conducted on the influence of climate on seabird biology (Durant et al., 2005), highlighting the need for more studies at regional scales. In the North Atlantic region, climatic conditions are strongly influenced at large spatial scales by variations in the North Atlantic Oscillation (NAO). This index is a measure of the difference in the pressure between the subtropical atmospheric high-

pressure zone centered over the Azores and the atmospheric low-pressure zone over Iceland (Ottersen et al., 2001). The NAO provides an index of oceanographic and climatic conditions over a large spatial scale. For example, higher values of winter NAO indices are associated with warmer, wetter and windier conditions in northern Europe, while low values are associated with colder and less windy conditions (Hurrell, 1995). In the North Atlantic the NAO influences environmental variables such as sea temperature or the frequency of extreme weather events; these changes can impact different trophic levels in varying ways (Ottersen et al., 2001). Climate effects on seabirds occur through two main processes: either directly through physiological effects, or indirectly through an influence on prey availability (Gremillet and Boulinier, 2009). The effect of climate change on seabird populations may take many years to become apparent (Thompson and Ollason, 2001) therefore, because this effect is so complex, it is necessary to conduct an in-depth study of the food web and its many different relationships with the environment in order to understand the causal mechanisms involved.

Direct influences of climate on seabirds

Climate variability influences environmental conditions such as sea temperature or the frequency of extreme weather events (Ottersen et al., 2001); however while changes in sea temperature indirectly affect seabirds by influencing food availability (Österblom et al., 2006), direct climate effects are likely to influence seabird ecology through impacts on reproductive output, mortality rates, and energetic costs (Schreiber, 2001). For example shoreline nesting seabirds are currently undergoing declines in breeding numbers due to successive years of poor breeding caused by nests being washed away by tidal surges, alongside the effects of predation and human disturbance (Mitchell, 2006). Moreover, increased frequency of storms and intense rainfall can negatively impact upon adult

survival (Frederiksen et al., 2008b) and lead to increased egg loss and chick mortality (Aebischer, 1993; Durant et al., 2005). In addition, the increases in wind speed can affect the cost of flight, which, in turn, leads to variations in foraging costs. However, this effect is species-specific and depends upon wing morphology and flight style (Spear and Ainley, 1997) such that gliding species like Northern fulmar *Fulmarus glacialis* (L.) and wandering albatross *Diomedea exulans* (L.) experience reduced energetic costs in windy conditions (Furness and Bryant, 1996; Weimerskirch et al., 2012), whilst flapping species such as little auks *Alle alle* (L.) experience the reverse (Gabrielsen, et al., 1991).

Indirect influences of climate on seabirds

Indirect climate effects on seabird populations are typically mediated via changes in the availability of food (Schreiber, 2001). This is normally manifested via bottom-up control where climate-mediated changes in the availability of lower trophic level prey (Beaugrand et al., 2000) have knock-on consequences for higher trophic level predators (Ottersen et al., 2004a, Frederiksen et al., 2006). In the marine environment prey populations (i.e. small pelagic fish) fluctuate in response to climatic change creating match-mismatch events (Wanless et al., 2005; Suryan et al., 2006; Durant et al., 2007; Cury et al., 2008) in which the spatio-temporal availability of the food resources necessary to predators is modified (Edwards and Richardson, 2004).

In the Northeast Atlantic, the impact of climate change on phytoplankton and zooplankton communities has already been demonstrated to be associated with changes in sea temperature and NAO (Planque and Fromentin, 1996; Fromentin and Planque, 1996; Beaugrand et al., 2000, 2002; Edwards et al., 2001; Richardson and Shoeman, 2004) leading to significant biogeographical shifts in zooplankton communities (Otteresen et al., 2001; Beaugrand et al., 2002; Beaugrand, 2005). Such reorganizations are termed ‘regime

shifts' and represent a persistent radical shift in the composition or productivity of marine communities, occurring at multiple trophic levels and on a geographical scale (Bakun, 2004). As a consequence of the establishment of warmer water conditions in the Northeast Atlantic, primary and secondary productivity have been dramatically modified (Beaugrand et al., 2002, Beaugrand, 2004), with dramatic effects upon seabird populations via bottom-up control (Mavor et al., 2005; Frederiksen et al., 2006). Such bottom-up control can lead to a scarcity of natural high-energy prey forcing seabirds to supplement their diet with lower energy food sources, which can negatively affect their reproductive success (Wanless et al., 2005).

1.4 SEABIRDS-FISHERY INTERACTIONS

Commercial capture fishing is one of the most pervasive anthropogenic activities that impacts upon the marine ecosystem (Pauly et al., 2002, 2005). Industrial fishery expansion has had global impacts on sustainability and has transformed the structure and function of marine food webs via top-down control by removing top predators (Pauly et al., 1998). The overexploitation of fish communities has depleted some fish stocks to near extinction (Casey and Myers, 1998), and it is predicted that there will be a collapse of worldwide fish stocks by 2048 (Stockstad, 2006). As well as reduced stocks of many commercial species, fisheries have also had wider direct and indirect ecosystem level impacts, for example the increasing mortality of by-catch species such as dolphins, turtles and seabirds (Alverson et al., 1994; Tasker et al., 2000; Lewison and Crowder, 2003; Read, 2008; Bryan et al., 2010), which are already considered as highly vulnerable, in addition to biodiversity reduction and loss of habitat (Jennings and Kaiser, 1998; Rogan and Mackey, 2007).

Direct effects of fisheries on seabirds

The direct effects of fisheries affect seabirds in quite different ways, but the main effect is via the direct impact on food availability by exploiting their most important prey (Furness and Camphuysen, 1997), which can lead to direct competition, especially when resources are limited (Furness, 1982; Furness and Birkhead, 1984; Montevecchi, 2002; Cowx, 2003; Frederiksen et al., 2004a; Karpouzi et al., 2007).

Although many oceanic or pelagic seabirds feed extensively on cephalopods or crustaceans, most continental shelf or shallow-sea seabirds feed predominantly on small pelagic schooling fish, such as sprat *Sprattus sprattus* (L.), lesser sandeel *Ammodytes marinus* (R.) and small herring *Clupea harengus* (L.) during the breeding season (Furness, 1990). In the North Atlantic small, lipid-rich shoaling fish are targets for industrial fisheries, and are largely utilized for the production of fish meal and fish oil; however the overexploitation of these fish stocks has had dramatic negative effects upon seabirds, influencing their productivity (Furness, 2003).

Indirect effects of fisheries on seabirds

Commercial fisheries can also have indirect effects upon marine top predators by modifying their demography and behavior (Furness 2003; Lewison et al., 2004). Discards (or discarded catch) represent that portion of the total food in the catch, in the form of bait, undersized catch and offal, which is thrown away or dumped at sea. There is a positive relationship between scavenging seabird populations and discards, as discards provide an additional source of food for some species, with less expenditure of energy than active predation (Furness, 1999; Garthe et al., 1999), and one that would otherwise be unavailable to them (Furness et al., 1988; Votier et al., 2004a). In fact, where discards were reduced scavenging seabirds have been shown to be negatively impacted (Oro et al., 1995; Oro and

Pradel, 2000; Furness, 2003), and in some cases the production of large quantities of discards may favour some seabird species (Votier et al., 2010). If discards decline this may indirectly lead to adverse impacts upon smaller seabird species, as the large generalist predatory seabirds, that tend to rely on discards, have been shown to switch feeding strategies from fish to small seabirds in the face of food shortages (Phillips et al., 1999; Votier et al., 2004b). The practice of discarding is widely regarded as running counter to fisheries and marine conservation objectives worldwide (Enever et al., 2009). Global discards are estimated to be around seven million tonnes per year (Kelleher, 2005), and this has led to the proposal of a discards ban in the most recent EU Common Fisheries Policy (CFP) in 2008 (currently in reform since 2009). However, it is difficult to predict the potential effects of reducing discard production on seabird populations, or whether scavenging behavior represents an 'ecological trap' (Gremillet et al., 2008a).

Another negative consequence of commercial fishing is the increase of seabird accidental mortality due to the fishing methods and gear utilized (Belda and Sanchez, 2001; Tuck et al., 2003). This phenomenon known as 'bycatch' occurs when scavenging seabirds become accidentally hooked or entangled and then drowned in fishing gear, and this has emerged as a major seabird conservation issue (Lewison et al., 2004; Anderson et al., 2011). In addition, monofilament gillnets also represent a serious hazard for pursuit diving seabirds (Tasker et al., 2000) and there are several examples where regional populations of seabirds have declined as a result of high mortality rates (Furness, 2003). Seabirds can also become entangled in lost or discarded fragments of fishing gear; Northern gannets *Morus bassanus* and various cormorant species will collect such material to use in nest construction, which can lead to the entanglement of both adults and chicks (Votier et al., 2011).

1.5 CONCLUSIONS

Marine ecosystems can be modified by impacts that affect the lowest and highest trophic levels, and these impacts can be propagated via bottom-up or top-down control, with dramatic consequences upon apex predators (Frederiksen et al., 2007b). Because of the complex interactions between human-induced climate change and fisheries, in addition to high variability from a global to regional scale, it is very difficult to disentangle the key drivers of ecosystem dynamics and this urgently needs clarification. Given the current pressures on marine ecosystems, and the likely increases in such pressures in the future due to growing human needs and a changing climate, it is imperative to improve our understanding of human impacts. In order to achieve these objectives, a comprehensive approach is necessary to account for both fisheries and climate impacts. In recent years, complex ecosystem-based approaches for fisheries management have been recognized as the most efficient way to achieve the goal of sustainable fisheries and biodiversity protection (Link, 2002; Garcia et al., 2003; Pikitch et al., 2004). Despite the growing attention to this type of complex approach, relatively few studies have specifically used this technique with respect to seabirds in the Northeast Atlantic (Aebischer et al., 1990; Carscadden et al., 2002; Hunt et al., 2002; Frederiksen et al., 2006; Luckzac et al., 2011), and to the best of our knowledge no such studies have been applied to the Celtic Sea ecosystem.

1.6 AIMS OF THE THESIS

The aim of the thesis is to investigate the effects of climate change and fisheries on the Celtic Sea ecosystem with focus on the response of seabirds. The current and future

impacts on the Celtic Sea food web will be studied using different modelling approaches and different geographical scales.

In **Chapter 2** a multiple trophic-level modelling approach is implemented for a large seabird colony in the Celtic Sea (Skomer) with the purpose of investigating the effects of climate change on the pelagic food web in the region. Using data collected during 1986 - 2007 direct and indirect 'bottom-up' climate effects across four trophic levels (phytoplankton, zooplankton, mid-trophic level fish (herring) and apex predators (four species of seabirds)) are examined.

In **Chapter 3** a similar approach is applied, increasing the geographical scale in a multiple-colony study in order to examine the effect of spatial variability and climate change across four trophic levels (phytoplankton, zooplankton, fish larvae and seabird (Black-legged kittiwake, *Rissa tridactyla*) in three regions around southwest Britain: the Irish Sea, the Celtic Sea and the English Channel.

In **Chapter 4** the trophic structure of the Celtic Sea ecosystem and the trophic role of seabirds are described successively by the application of an ecosystem-based mass-balance model Ecopath (which belongs to Ecopath with Ecosim). This study contributes significantly to our understanding of the organization and trophic transfers between biological groups within this ecosystem.

On the basis of the results obtained in the previous chapter, in **Chapter 5** policy exploration analysis under current and future fisheries and climate scenarios is conducted

by using the tropho-dynamic model Ecosim in order to provide guideline support for resources management and seabird conservation in the Celtic Sea.

In **Chapter 6** the various threads explored in the thesis are brought together, the main findings discussed and opportunities for further research are placed into a broader context.

Chapter 2

Influence of climate change and trophic coupling across four trophic levels in the Celtic Sea

Abstract

Climate change has had profound effects upon marine ecosystems, impacting across all trophic levels from plankton to top predators. Determining the impacts of climate change on marine ecosystems requires understanding the direct effects on all trophic levels as well as indirect effects mediated by trophic coupling.

The aim of this study was to investigate the effects of climate change on the pelagic food web in the Celtic Sea, a productive shelf region in the Northeast Atlantic. Using long-term data, we examined possible direct and indirect 'bottom-up' climate effects across four trophic levels: phytoplankton, zooplankton, mid-trophic level fish and apex predators (seabirds).

During the period 1986-2007, although there was no temporal trend in the North Atlantic Oscillation index (NAO), the average annual Sea Surface Temperature (SST) in the Celtic Sea increased by 0.66 ^{o}C. Despite this, there was only a weak signal of climate change in the Celtic Sea food web, with indirect bottom-up effects on mid-trophic level fish and seabirds. Changes in plankton community assemblage were found, however this was not related to SST or NAO. The abundance of herring *Clupea harengus* was significantly negatively correlated with spring SST, suggesting a direct climate effect. Seabird demographics showed complex species-specific responses. There was evidence of direct

effects of spring NAO (on black-legged kittiwake *Rissa tridactyla* population growth rate) as well as indirect bottom-up effects of lagged spring SST on razorbill *Alca torda* breeding success. Negative relationships between razorbill and common guillemot (*Uria aalge*) breeding success and population growth rate may be explained by interactions between mid-trophic level fish.

Our findings show that the impacts of climate change on the Celtic Sea ecosystem are not as marked as in nearby regions (e.g. the North Sea), emphasizing the need for more research at regional scales in order to understand how climate change is impacting upon the marine environment.

2.1 INTRODUCTION

Human-induced climate change has profoundly impacted marine ecosystems across the globe. These impacts have had wide-ranging effects upon the physiology, distribution, phenology and abundance of species, resulting in long-term threats to biodiversity (Guldberg and Bruno, 2010). A key feature of these climate-induced impacts is a high degree of spatial heterogeneity (Beaugrand et al., 2009, McGinty et al., 2011). Understanding the nature of this variation is a key goal for assessing and mitigating the impacts of global climate change.

Environmental change may impact different trophic levels in varying ways (Frederiksen et al., 2006, Osterblom et al., 2006), such that marine food webs may be impacted both directly and indirectly (Ottersen et al., 2001). Direct effects of climate change include the influence of temperature change, particularly for ectothermic organisms (i.e. fish and invertebrates), or extreme weather events, which can impact endothermic organisms

(Frederiksen et al., 2008b). Taken together these direct effects can influence physiology, morphology and behaviour, leading to a suite of emergent ecological responses (Harley et al., 2006). Indirect effects are typically mediated via trophic coupling. This is normally manifested via bottom-up control where climate-mediated changes in the availability of lower trophic levels have knock on consequences for higher trophic levels (Ottersen et al., 2004b, Frederiksen et al., 2006). Marine higher trophic level predators can also govern the abundance of lower trophic levels by top-down control (Cury et al., 2000), or mid-trophic level species may exert both top-down and bottom-up effects in a process known as wasp-waist control (Fauchald et al., 2011). It is still unclear, however, how the nature of these effects, as well as ecosystem responses, varies across regions (Aebischer et al., 1990; Hunt et al., 2002).

The aim of this study was to look for climate-related influences across four trophic levels in the Celtic Sea, a productive shelf region in the northeast Atlantic. This is an extremely important area in terms of fish and invertebrate biodiversity (Ellis et al., 2002) and it supports a large community of apex predators in the form of seabirds (Mitchell et al., 2004) and marine mammals, as well as several important European fisheries (Pinnegar et al., 2002). Profound climate-mediated changes in the nearby North Sea have led to concerns about the long-term viability of certain populations of apex predators (Frederiksen et al., 2006, Wanless et al., 2007), so a key question is to determine how climate change might be impacting the Celtic Sea food web. This region is quite different from the North Sea in terms of physical characteristics and oceanography (i.e. general circulation pattern, depth, sea temperature, OSPAR, 2000; OSPAR, 2002) and this may influence trophic responses to climate change.

Direct and indirect effects of climate across four trophic levels were tested. Direct climate effects at each level of the food web were expected via a significant correlation between abundance/biomass/demography and environmental variables: the North Atlantic Oscillation index (NAO) and Sea Surface Temperature (SST). The NAO strongly influences the frequency of extreme weather events, which may directly impact some seabirds (Frederiksen et al., 2008b). SST may have direct effects through changes to the biology and distribution of ectothermic fish and invertebrates (Ottersen et al., 2001).

Indirect effects were expected via bottom-up processes, characterised by a positive correlation between a measure of predator abundance/biomass/demography and prey. We also tested for potential top-down effects typified by a negative correlation between predator and prey. We modelled the Celtic Sea pelagic food web simplified into four trophic levels: four species of seabird (black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge*, razorbill *Alca torda* (L.) and atlantic puffin *Fratercula artica* (L.)), pelagic fish (Atlantic herring *Clupea harengus*), zooplankton and phytoplankton. For each level, long-term data from 1986 to 2007 were collated and analysed along with measures of environmental conditions (SST and NAO).

2.2 MATHERIALS AND METHODS

Study area

The Celtic Sea is an area of the northeast Atlantic continental shelf, southwest of the United Kingdom (Figure 2.1). It represents a transition zone between the Atlantic Ocean and coastal waters of the Bristol Channel and Irish Sea. There is a persistent north-westwards current running from Brittany to the Bristol Channel, as well as oceanographic fronts (the

Irish Shelf, the Celtic Sea and Ushant fronts), which tend to inhibit lateral dispersal of phytoplankton (OSPAR, 2002).

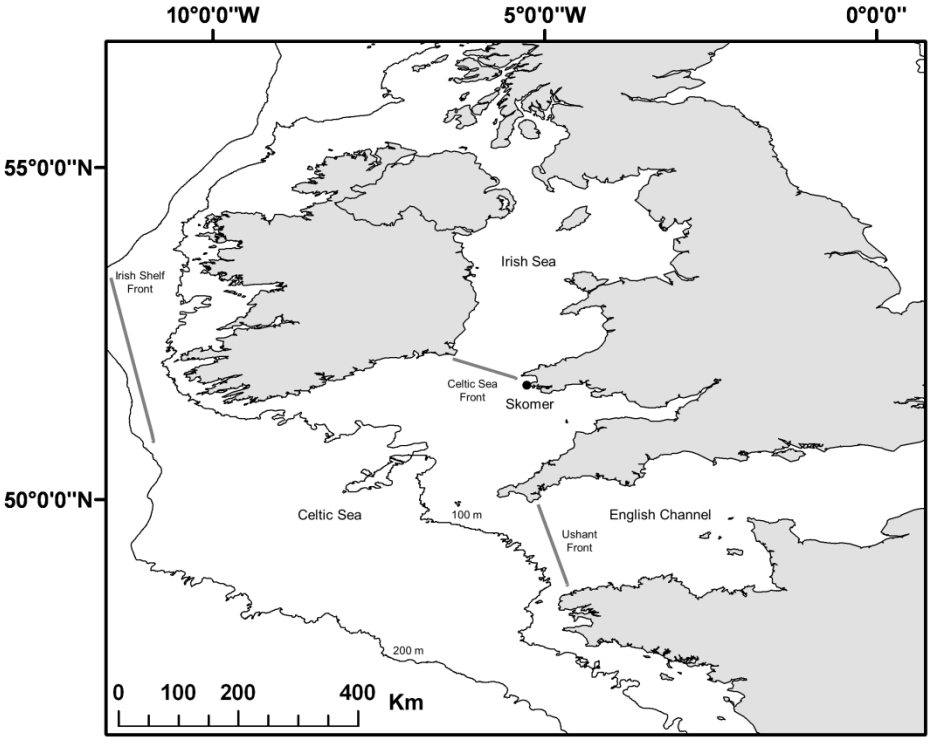

Figure 2.1 The Celtic Sea, including oceanographic features (adapted from OSPAR, 2000) and the seabird colony investigated in this study (Skomer Island: 51 º 40N, 05 º 15W). The Irish Shelf Front occurs to the south and west of Ireland and exists all year-round. This front marks the boundary between waters of the shelf (often mixed vertically by the tide) and offshore North Atlantic waters. In addition there are two seasonal fronts systems which tend to develop during spring: the Celtic Sea front (dividing the Celtic Sea from the Irish Sea) and the Ushant Front, which develops from the coast of Brittany and extends to the western English Channel (dividing the Celtic Sea from the English Channel).

Phytoplankton

The annual phytoplankton bloom in the Celtic Sea typically occurs from April to October (ICES, 2008). Continuous Plankton Recorder (CPR) data suggest a steady increase in phytoplankton abundance over at least the last 20 years (ICES, 2008). Phytoplankton productivity and taxonomic composition in the Celtic Sea depend on water column structure: diatoms dominate areas with high nutrient content and display high rates of productivity, while dinoflagellates and microflagellates are found in stratified waters exhibiting lower rates of productivity. Productivity is reasonably high on the shelf with a rapid decrease west of the shelf break (ICES, 2008).

Zooplankton

In the Celtic Sea the zooplankton community is dominated by the large copepod *Calanus helgolandicus* (C.) (Planque and Fromentin, 1996); CPR data suggest an overall decline in the abundance of zooplankton with *Calanus* abundance falling below the long term mean (ICES 2008). Long-term studies reveal that spatial patterns of zooplankton have changed significantly over the past 40 years, possibly as a result of climate-related reorganization of the zooplankton (Pitois and Fox, 2006). The ecological mechanism responsible for these changes remains unclear, however, and further analysis of CPR data in relation to environmental change is needed to clarify the situation.

Pelagic fish

This region is characterized by high fish diversity and it is an important spawning ground for many species (Ellis et al., 2002). Like many coastal seas, the size-structure of the fish community has changed significantly over recent decades: there has been a decrease in the relative abundance of larger fish with a concomitant increase in the numbers of smaller fish (Pinnegar et al., 2002). Henderson (2007) reports two main events in the 1980s and 1990s

representing changes in the fish community composition, coinciding with climate-induced changes of plankton community in some regions of the North Atlantic (Beaugrand et al., 2009).

Seabirds

The Celtic Sea is an extremely important area for seabirds, supporting ~300,000 breeding pairs of 15 species (Mitchell et al., 2004), including internationally important populations of northern gannet *Morus bassanus* and Manx shearwater *Puffinus puffinus*, as well as nationally or regionally important populations of common guillemot *Uria aalge*, lesser black-backed gull *Larus fuscus* (L.), herring gull *Larus argentatus* (P.), black-legged kittiwake *Rissa tridactyla*, Atlantic puffin *Fratercula artica* and razorbill *Alca torda*.

Environmental variables

Two environmental predictors were used to test for direct and indirect effects of climate change: the North Atlantic Oscillation (NAO) and Sea Surface Temperature (SST). The description of the ecological mechanism associated with each climate predictor is summarized in Table 2.1.

Table 2.1 Potential climate effects for four trophic levels in the Celtic Sea. Direct effects are manifest by correlations between climatic predictors and one of the ecological descriptors. Indirect effect links ecological descriptors to climate only through its effect on another trophic level i.e. via trophic coupling.

Trophic level	Climate variable	Type of effect	Parameter related to climate variability	Suggested mechanism	Climate predictor used in this study	Reference
Phytoplankton	NAO	Direct	Abundance	Not defined possible effect of mixing waters	Winter NAO	Edwards et al., 2001 Reid et al., 1998
	SST	Direct	Abundance/distribution	Effect of nutrients availability, metabolic rates and water stratification	Winter SST	Richardson and Shoeman, 2004
Zooplankton	NAO	Direct	Abundance	Water mixing, increase of turbulence	Winter NAO	Beaugrand et al., 2000 Planque and Fromentin, 1996
	SST	Direct	Abundance/distribution	Increase in water temperature	Winter SST	Beaugrand et al., 2002 Fromentin and Planque, 1996
Pelagic fish	NAO	Indirect	Abundance/food availability	Changes in temperature and wind patterns causing regime shift, changes in the pattern of transport of herring in the North Sea	Winter NAO	Alheit and Hagen, 1997 Corten, 1999
	SST	Direct	Spawning, recruitment, distribution	Alteration of physiological rates (eggs hatching, larvae and juvenile stages)	Lag Spring SST	Toresen et al., 2001 Toresen and Ostvedt, 2000 Cardinale et al., 2004 Collas et al., 2007
Seabird	NAO	Direct	Survival, reproductive output	Increase of storm frequency influencing foraging ability or chick impacts with impacts on reproductive output	Spring NAO	Frederiksen et al., 2008b Durant et al., 2005 Aebischer et al., 1993 Votier et al., 2005, 2008
	SST	Indirect	Food availability	Effect on pelagic fish	Lag Spring SST	Frederiksen et al., 2006

NAO influences water circulation and sea temperature, which can result in changes to plankton communities (Beaugrand et al., 2000). These changes are likely to have effects upon higher trophic levels such as fish and seabirds by influencing food availability (Österblom et al., 2006) or affecting wind, rainfall and air temperature which may consequently influence seabird populations through survival, e.g. by increasing extreme events occurrence (Aebischer, 1993; Frederiksen et al., 2008b).

Two different versions of the NAO index were used in this study: spring NAO during the seabird breeding season (SNAO, March-June) and winter NAO (WNAO, December-March) in order to test respectively for direct and indirect effects of climate change. Monthly data from 1986 to 2007 were downloaded from the University Corporation for Atmospheric Research (UCAR) website, Climate Analysis section http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatmon) and an annual value for each index calculated (Fig. 2.2 a, b).

Variation in SST can affect the marine ecosystem from plankton communities (Planque and Fromentin, 1996), to mid-trophic level fish (Attrill and Power, 2002; Ottersen et al., 2004b), up to apex predators such as seabirds (Durant et al., 2003) via match-mismatch events between predators and prey (Aebischer et al., 1990; Hunt et al., 2002). Both winter and spring SST (WSST, December-March; SSST, March-June) were used as climate predictors. WSST was used to test for direct effects on plankton, and lagged SSST (1-2 years) to test for direct and indirect effects on pelagic fish and indirect effects on seabirds (Table 2.1-2.2). SST data were derived from satellite images and collated from the POET database available at http://poet.jpl.nasa.gov with a spatial resolution of 0.04º longitude x 0.04º latitude (approximately 4 x 4 km).

Plankton data

The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) hosts the Continuous Plankton Recorder (CPR), the world's largest plankton dataset, which SAHFOS has been collecting since 1931 (see Richardson et al., 2006). This dataset represents a consistent semi-quantitative index of phytoplankton and zooplankton abundance and has recorded seasonal and annual changes in plankton communities (e.g. Frederiksen et al., 2006; Beaugrand et al., 2009).

In the present study, a total of 2299 CPR samples, taken between 1986 and 2007, were analysed to investigate possible changes in the plankton community in the Celtic Sea. The abundance of diatoms and copepods was determined in each sample and annual means calculated by averaging across samples taken in the period March-June for the Celtic Sea (49ºN-53º, 4ºE-10ºW). Copepod biomass was calculated by multiplying the abundance of each copepod taxon (mainly calanoid; 28 in total between species and taxonomic group) by its average mass estimated from an allometric relationship based on size (Richardson et al., 2006).

Diatom abundance was used as a proxy of copepod food availability (Frederiksen et al., 2006), and copepod biomass was used as a proxy for pelagic fish prey. Copepods were divided into two groups: small copepods (<2mm) and large copepods (>2mm) because of changes in pelagic fish diet such as Atlantic herring (hereafter, herring) during different life stages. Young herring (1 year old, ≤10 cm Total Length (TL); hereafter 0-group) prefer smaller copepods (<2 mm) while older herring (> 1 year old, ≤15 cm TL; hereafter 1-group) feed mainly upon larger size copepods (>2 mm) (Brander et al., 2003).

Fish data

Mid-trophic level fish are vectors for the transfer of energy from low trophic levels to apex predators (Cury et al., 2000). In this study long-term data describing herring 0- and 1-group abundance were used as a proxy for seabird food availability. Data spanned the period 1986-2007 and were extracted from the Herring Assessment Working Group (HAWG-ICES) acoustic survey designed to evaluate the state of pelagic fish species (sprat *Sprattus sprattus* and herring) around the UK coasts and, in particular, herring stock in the Celtic Sea (ICES 2010; Fig. 2.2 f).

Long-term data on other small pelagic fish such as sprat or lesser sandeels (*Ammodytes* spp.) (hereafter, sandeel) were not available for the region. Nevertheless, data from the Centre for Environment Fisheries and Aquaculture Science (CEFAS) ground fish survey (trawl survey designed to study the distribution, composition and abundance of all fish, commercial shellfish and cephalopod species in the Celtic Sea) has shown that sprat and herring are often caught together; these pelagic species can be also considered ecologically equivalent (with similar habitats and diet composition) (Voss et al., 2009). In order to test if herring was a good proxy of small pelagic fish species in the Celtic Sea, we analysed the occurrence of sprat and herring in the environment by using the only dataset available of landings from CEFAS ground fish surveys (Parent, 2011) covering the period 1986-2002. This showed that these two species seem to have similar fluctuations in the Celtic Sea region (Supplementary material, Appendix 1, Figure A1.1). Herring is one of the most abundant planktivorous fish in the Celtic Sea, and juvenile stages (0- and 1-group) along with other small schooling pelagic fish, such as sandeel or sprat, are an important prey of many seabird species (Frederiksen et al., 2007a). In the Celtic Sea herring juveniles tend to remain in shallow coastal areas (nursery) for the first two years of their lives (ICES, 2010).

Studies on guillemot diet on Skomer evidenced that they feed mainly upon sprat and juvenile herrings (Birkead et al., 2007). For these reasons we believe that herring (0- and 1-group) represents a good proxy for seabird food availability.

Seabird data

Data on breeding success and population estimates of four piscivorous seabirds were were extracted from the Seabird Monitoring Programme Database at www.defra.jncc.gov.uk/smp: black-legged kittiwake (hereafter kittiwake), common guillemot (hereafter guillemot), razorbill and Atlantic puffin (hereafter puffin) breeding on Skomer Island, Wales (51º 40N, 05º15W; Fig. 2.1). These data spanned the period from 1986 to 2007 (Fig. 2.2 g-n) with 22 years for kittiwake, 19 for guillemot, 15 for razorbill and 20 for puffin.

These four seabirds are characterised by different foraging and reproductive strategies. Kittiwakes are surface feeders and lay an average of 3 eggs per breeding attempt, while guillemots, razorbills and puffins are all pursuit divers and lay a single egg (Mitchell et al. 2004). These four species also differ somewhat in their foraging range: kittiwake, razorbill and guillemot forage mainly inshore (Ainley et al., 2003; Benvenuti, 2001; Clarke et al., 2003), whilst puffins tend to forage further offshore (Hatch et al., 2000). The species also differ in their prey loading: kittiwakes, puffins and razorbills are multiple prey-loaders whereas guillemots are single prey-loaders. Given these ecological differences and their possible diverse vulnerability to food shortage and hence climate change, we modelled their responses separately.

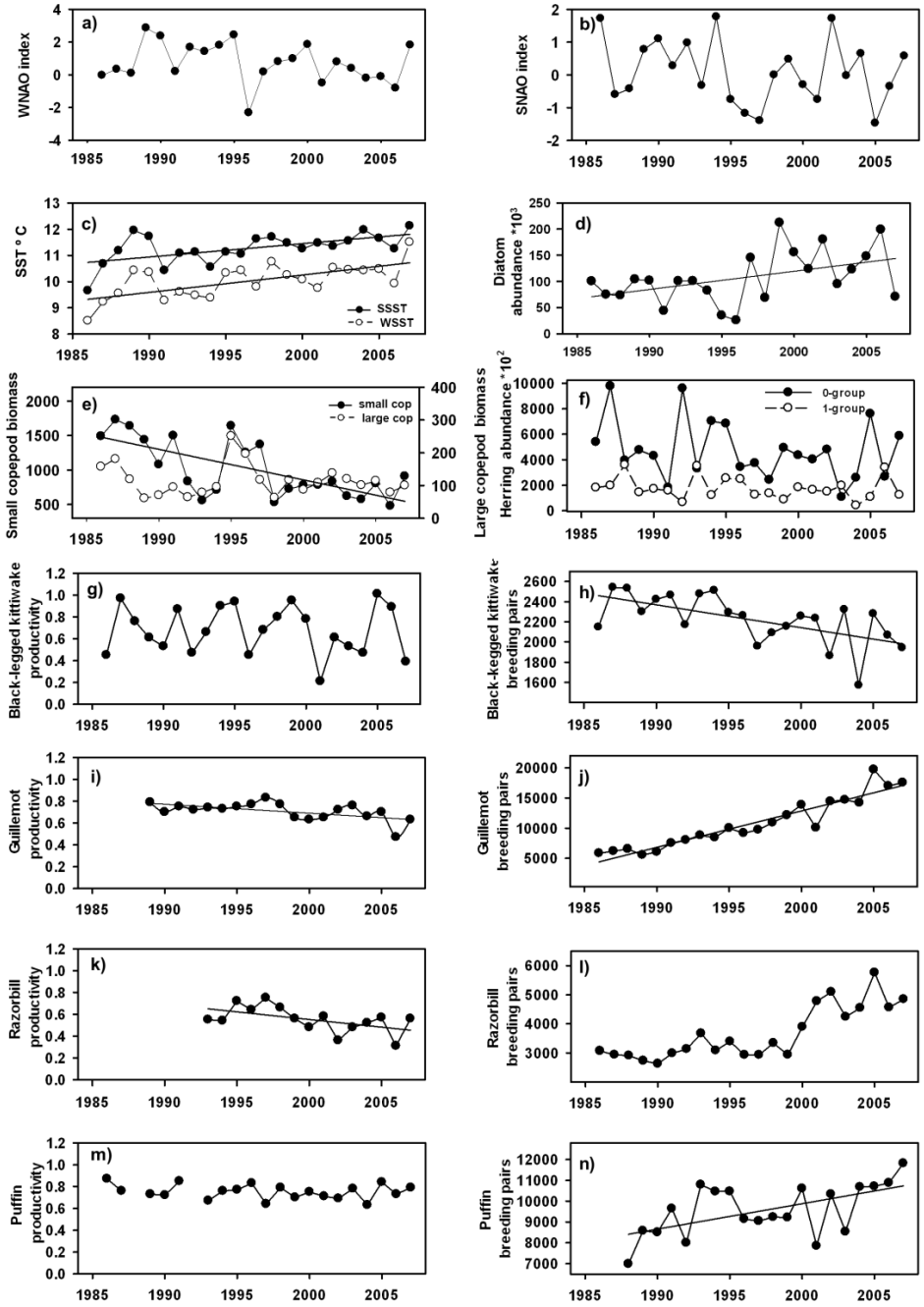

Figure 2.2 Variables used for model construction: Winter NAO index (a); Spring NAO index (b); Sea Surface Temperature (ºC) (c); Diatom abundance (d); small and large copepods biomass (mg wet weight) (e); Herring 0- and 1-group abundance (f); Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size) (g) and population count (h); Common guillemot productivity (number of fledged chicks per breeding pair, weighted for sample size) (i) and population count (j); Razorbill productivity (number of fledged chicks per breeding pair, weighted for sample size) (k) and population count (l); Atlantic puffin productivity (number of fledged chicks per breeding pair, weighted for sample size) (m) and population count (n). Fitted linear regressions indicate significant temporal trends.

Model construction and statistical analyses

Colinearity among explanatory variables may increase the probability of type I errors, therefore we tested for possible temporal trends in our data using linear regression. Multiple regression models were used to identify the main predictors for each trophic level (diatoms, copepods, herring and seabirds). When the dependent variable was not normally distributed, it was $\log_e$ transformed. For the four seabird species two demographic rates were used: (1) productivity (breeding success) expressed as the number of fledged chicks per breeding pair, weighted by the number of pairs sampled and (2) population growth rate (R_t), which was calculated from the time series as $\log_{10}(N_{t+1})$-$\log_{10}(N_t)$ (Royama 1996).

The following explanatory environmental variables were examined: (1) spring NAO and winter NAO to test for direct and indirect climate effects (spring NAO for seabirds, winter NAO for plankton and fish); (2) winter SST for plankton, lagged spring SST (1,2 years lag) for pelagic fish to test for direct climate effects on each age class, lagged spring SST (1 year lag) to test for indirect climate effects on seabirds. When there was a temporal trend in the dependent variable, year was included as a continuous covariate. The variables used for the model construction are shown in Table 2.2.

Starting from the full model, the most parsimonious model for each trophic level was selected on the basis of the lowest Akaike Information Criterion (AIC), corrected for small sample size (AICc). This approach selects the model with the best balance between bias and precision and avoids problems of, for example, multiple testing among explanatory variables (Burnham and Anderson 2002). A set of candidate models was compared using difference in AIC_c between the top-ranked and current model (delta AIC_c), and by calculating the AIC_c weight (the scaled likelihood that each model is the best description of the data; Burnham and Anderson 2002). Competing models were selected when having

their AIC_c within 2 of the minimum (Burnham and Anderson 2002) and are presented in Tables A1.2-1.4 (Supplementary material, Appendix 1). The importance of each predictor was evaluated using evidence ratios, calculated by summing the Aikaike weights for all the models where the effect appeared and dividing by the summed Aikake weights for models without the effect (Burnham and Anderson, 2002). Aikaike weights estimate the probability that the given model provides the best description of the data, given the set of models considered, and evidence ratios summarize this for individual effects, again conditional on the model set. Evidence ratios > 10 indicate moderately strong support for the effect (Lukacs et al., 2007).

Model goodness of fit was compared using the deviance and coefficient of determination (R^2). Covariates were considered statistically significant when the p value was <0.05. Model residuals were evaluated to assess general model performance; in particular statistical tests were applied to test for non-normality (Shapiro-Wilk), heteroscedasticity (Breush-Pagan) and autocorrelation of errors (Durbin-Watson). All modelling was carried out using R version 2.8 (R Development Core Team, 2010).

Table 2.2 Response variables and predictors used for multiple regression models. For each response variable the full model is also given. WNAO: winter North Atlantic Oscillation index; SNAO: spring North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; 2lag-SSST: 2 years lagged spring Sea Surface Temperature; Small cop: small copepods (<2mm); Large cop: large copepods (>2mm); Her 0-g: herring 0-group; Her 1-g: herring 1-group; BS: Breeding Success expressed as the number of fledged chicks per breeding pair, weighted for sample size; R_t: Population growth rate.

Response Variable	Direct climate effect	Indirect climate effect	Food availability	Full model
Diatom	WNAO; WSST			WNAO + WSST + year
Small cop	WNAO; WSST		Diatom	WNAO + WSST + diatom + year
Large cop	WNAO; WSST		Diatom	WNAO + WSST + diatom + year
Her 0-g	1-lag SSST	WNAO	Small cop+ large cop	WNAO + 1lag-SSST + small cop + large cop + year
Her 1-g	2-lag SSST	WNAO	Small cop + large cop	WNAO + 2lag-SSST + small cop + large cop + year
Kittiwake BS	SNAO	1lag-SSST	Her 0-g	SNAO + 1lag-SSST + her 0-g + year
Kittiwake R_t	SNAO	1lag-SSST	Her 0-g	SNAO + 1lag-SSST + her 0-g + year
Guillemot BS	SNAO	1lag-SSST	Her 0-g+ her 1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year
Guillemot R_t	SNAO	1lag-SSST	Her 0-g+ her1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year
Razorbill BS	SNAO	1lag-SSST	Her 0-g+ her 1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year
Razorbill R_t	SNAO	1lag-SSST	Her 0-g + her1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year
Puffin BS	SNAO	1lag-SSST	Her 0-g + her 1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year
Puffin R_t	SNAO	1lag-SSST	Her 0-g + her1-g	SNAO + 1lag-SSST + her 0-g + her 1-g + year

2.3 RESULTS

Correlations between covariates

Preliminary explanatory analyses showed that weak correlations occurred in some cases (Supplementary material, Appendix 1, Table A1.1); however no significant correlation was found between the environmental variables (both winter and spring measures of NAO and SST) and the other covariates, with the exception of weak positive correlation between kittiwake R_t and spring NAO (r = 0.43; p = 0.04), and a negative correlation between puffin and spring SST (r = 0.50; p = 0.02).

Environmental variables

Temporal trends in environmental variables (winter NAO, spring NAO; winter and spring SST) are shown in figures 2.2a-c. There was no linear trend for either spring or winter NAO over time, but there was considerable inter-annual variability. SST increased significantly over time (winter SST: p <0.001, slope = 0.006±0.01; spring SST: p = 0.004, slope = 0.05±0.01) with the minimum value in 1986 and the maximum in 2007 (8.5º C and 11.5º C for winter SST, 9.7º C and 12.1º C for spring SST respectively).

Phytoplankton

Diatom abundance increased over the period 1986-2007 (p = 0.03, slope = 3.47 ± 1.53; Fig. 2.2d). None of the environmental covariates (winter NAO or winter SST) explained a significant amount of the variation in diatom abundance (Table 2.3).

Zooplankton

Small copepod (<2 mm) biomass declined significantly over time (p = 0.003, slope = -0.03±0.01), but there was no significant trend in large copepods (>2mm; Table 2.3, Fig.

2.2e). Neither the environmental covariates nor diatom abundance were related to biomass of small or large copepods (Table 2.3).

Pelagic fish

Herring abundance fluctuated over time, with no clear linear trend (Fig. 2.2f). Both herring 0- and 1-group did not appear to be regulated by our measures of food availability (i.e. the biomass of small and large copepods; Table 2.3), but there was a weak negative climate effect for both groups, with 0-group herring showing a significant negative effect of 1 year lagged spring SST (p = 0.02, slope = -0.305±0.125) and 1-group herring a significant effect of 2 year lagged spring SST (p = 0.04, slope = -0.410±0.193; Table 2.3).

Seabirds

Kittiwakes showed highly variable reproductive success, ranging from 0.21 chicks pair^{-1} in 2001 to 1.01 chicks pair^{-1} in 2005 (Fig. 2.2g), but was not significantly correlated with any covariates (Table 2.3). The number of breeding pairs has declined significantly over the last 22 years (Fig. 2.2h; p = 0.002, slope = -22.71±6.62, R^2 = 0.34) and population growth rate (R_t) was significantly positively correlated with spring NAO (p = 0.03, slope = 0.0314±0.014).

Guillemot productivity declined over time (p = 0.009, slope = -0.008±0.002, R^2 = 0.30): the highest productivity was in 1997 (0.83 chicks pair^{-1}) and the lowest in 2006 (0.47 chicks pair^{-1}; Fig. 2.2i), but was not significantly related to any covariates (Table 2.3). The number of breeding pairs increased significantly (p <0.001, slope = 425.5±95.3, R^2 = 0.51; Fig. 2.2j). Guillemot population growth rate was weakly negatively correlated with 1-group herrings (p = 0.04, slope = -0.352x10^{-6} ±0.161x10^{-6}).

Razorbill productivity declined over time (p = 0.04, slope = -0.01±0.06, R^2 = 0.23): the highest productivity was in 1997 (0.75 chicks pair^{-1}) and the lowest in 2006 (0.31chicks pair^{-1}) (Fig. 2.2k). Razorbill productivity was significantly negatively correlated with Spring SST lagged by 1 year (p = 0.01, slope = -0.144±0.05), spring NAO (p = <0.001, slope = -0.074±0.013) and with the abundance of group 1 herring (p = 0.003, slope = -0.884x10^{-6}±0.167x10^{-6}). The number of breeding pairs increased (Fig. 2.2l) despite no linear trend was found. Our most parsimonious population growth model included the intercept only (Table 2.3).

Puffin productivity did not show a temporal trend (p = 0.37, R^2 = -0.009) with an annual average of 0.75 chicks pair^{-1} (Fig. 2.2m), although the number of breeding pairs increased significantly over time (p = 0.008, slope = 122.2±41.8, R^2 = 0.29; Fig. 3.2n). None of the explanatory covariates was related to productivity or population growth rate (Table 2.3).

Table 2.3 Model selection to estimate factors influencing each trophic level. Only the best supported models are shown. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; Er: Evidence ratio; k: number of parameters in the model; R^2: adjusted coefficient. WNAO: winter North Atlantic Oscillation index; SNAO: spring North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; 2lag-SSST: 2 years lagged spring Sea Surface Temperature; her 0-g: herring 0-group; her-1g: herring 1-group; Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented.

Model selected	AICc weight	Er	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS								
Diatom abundance								
WSST + year	0.28	0.590	3	22	4.59	0.16	WSST 0.11 **year 0.02**	WSST -0.362 (±0.221) **year 0.054 (±0.022)**
PRIMARY CONSUMERS								
Small copepod biomass								
diatom + year	0.30	36.254	3	22	1.71	0.47	diatom 0.11 **year 0.003**	diatom -0.22 (±0.13) **year -0.03 (±0.01)**
Large copepod biomass								
diatom + WNAO	0.24		3	22	2.16	0.19	diatom 0.08 WNAO 0.10	diatom -0.250 (±0.13) WNAO -0.101 (±0.06)
SECONDARY CONSUMERS								
Herring 0-group abundance								
1-lagSSST + WNAO	0.20	0.895	3	22	4.00	0.25	**1-lagSSST 0.02** WNAO 0.11	**1-lagSSST -0.450 (±0.180)** WNAO 0.133 (±0.081)
Herring 1-group abundance								
2-lagSSST	0.24	0.672	2	22	4.60	0.15	**0.04**	**-0.41 (±0.19)**
APEX PREDATORS								
Black-legged kittiwake								
Productivity								
Intercept only	0.25		1	22	1.04		<0.001	
Population growth rate								
SNAO	0.32	2.120	2	22	0.07	0.16	**0.036**	**0.0314 (±0.014)**
Common guillemot								
Productivity								
year	0.23	22.726	2	19	0.07	0.29	**0.009**	**-0.008 (± 0.002)**
Population growth rate								
her 1-g + year	0.45	1.626	3	22	0.07	0.12	**her 1-g 0.042** year 0.557	**her 1-g -0.352x10^{-6} (±0.161x10^{-6})** year -0.001 (±0.002)
Razorbill								
Productivity								
1lag-SSST + SNAO + her 1-g + year	0.83	11.297 88.556 452.813 2407.998	5	19	0.02	0.82	**1-lagSSST 0.01** **SNAO <0.001** **her 1-g 0.003** **year 0.01**	**1-lagSSST -0.144 (±0.05)** **SNAO -0.074 (±0.013)** **her 1-g -0.884x10^{-6} (±0.167x10^{-6})** **year -0.01 (±0.003)**
Population growth rate								
her 1-g	0.23		2	22	0.09	0.12	her 1-g 0.09	her1-g -0.264x10^{-6} (±0.149x10^{-6})
Atlantic puffin								
Productivity								
intercept only	0.28		1	20	0.08	--	<0.001	
Population growth rate								
intercept only	0.28		1	20	0.09	--	0.578	

2.4 DISCUSSION

Our results showed both direct and indirect effects of climate change on the Celtic Sea food web, suggesting a weak climate impact from mid-trophic levels to seabirds. In particular, we found that despite changing environmental conditions in the Celtic Sea (i.e. SST is increasing), the response of organisms differed across trophic levels. Increasing SST, for example, had negative impacts on pelagic fish (herring), but did not influence copepods and only affected razorbill productivity. Possible mechanisms and explanations for these findings, as well as comparisons with climate related patterns in other regions are discussed below.

Direct Climate change effects on the Celtic Sea pelagic food web

Phytoplankton biomass in the North Sea and west of the British Isles has increased sharply during the mid-1980s in response to increasing SST (Beaugrand and Reid, 2003, Edwards et al., 2001). Our results show that diatom abundance in the Celtic Sea also increased during the period 1986 to 2007 (Fig. 2.2d), although in contrast to other regions in the northeast Atlantic this could not be directly linked with changes in climate predictors (winter NAO and winter SST).

Our study suggests that copepods biomass in the Celtic Sea were not significantly related to changes in SST and NAO (Table 2.3). As with phytoplankton, this is in contrast to the North Sea where calanoid copepods are positively correlated with winter NAO (Fromentin and Planque, 1996), although previous work has revealed strong regional variation in this relationship within the Northeast Atlantic (McGinty et al., 2011). Previously, Pitois and Fox (2006) argued that climate change had led to a structural reorganization of zooplankton communities in the Celtic Sea region during the period 1958-2003. Our lack of a strong climate signal in copepod biomass (Table 2.3) over the period 1986-2007 indicates that

either these changes occurred prior to the period of our study (1986-2007) , or it is only possible to detect a climate change signal over four decades.

Previous work has shown that both NAO and SST can strongly impact upon fish growth and abundance (Attrill and Power, 2002, Rijnsdorp et al., 2009). Our results did not indicate an effect of winter NAO on herring 0 and 1-group, although both age classes were negatively correlated with spring SST (Table 2.3). Increasing SST has been found to have both positive and negative effects on small pelagic fish in the Northeast Atlantic (Toresen, 2001; Cardinale et al., 2004). The response of herring to climate change is likely to be latitude-dependent with positive responses at high latitudes and negative at lower latitudes, such as in the Celtic Sea latitudes (Toresen and Østvedt, 2000). This negative effect is likely to be explained by the direct influence of sea temperature on herring spawning and recruitment.

We found a weak positive effect of spring NAO on black-legged kittiwake population growth rate and a weak negative effect on razorbill breeding success (Table 2.3). The main driver for this effect is unclear but may be related to the direct effects of wind-speed or storm-frequency (Votier et al., 2005; Frederiksen et al., 2008b), both of which are correlated with NAO. Under this scenario strong winds associated with positive NAO phases may differentially affect species such as kittiwake and razorbill because of variations in wing shape and foraging strategies.

Trophic coupling in the Celtic Sea

Our results suggest that during 1986-2007 both the plankton community and herring in the Celtic Sea were not strongly regulated via bottom-up forcing (Table 2.3). Given the strong increase in SST over this period (Fig. 2.2c), we had anticipated bottom-up control, because

this type of trophic linkage is often thought to be under the influence of climate, as in the nearby North Sea (Frederiksen et al., 2006). Regional variability in the strength of bottom-up control is common, however, and there is evidence that strong variation exists within the North Sea (Frederiksen et al., 2007a, McGinty et al., 2011).

In general there was no direct evidence that herring abundance was a limiting factor for seabirds in the Celtic Sea, instead a negative correlation between seabird demographics (guillemot R_t and razorbill breeding success) and herring abundance (Table 2.3) suggested top-down control. While we cannot exclude this possibility, an alternative explanation is that this age-class of herring may exert strong top-down effects on other pelagic fish such as sandeels that form an important part of the diet of these two Alcids. A similar trophic mechanism was previously proposed in the North Sea, where herring abundance was negatively correlated with sandeel stocks (Furness, 2004).

A significant negative relationship between razorbill productivity and spring SST lagged by one year (Table 2.3), suggests indirect bottom-up forcing, since SST is unlikely to directly impact razorbills, but may instead influence the availability of mid trophic level forage fish. Under this situation, SST might be a reliable proxy for overall abundance of forage fish, rather than herring abundance alone. It is unclear why this effect was not shown by the other seabird species, but differences in foraging range and behaviour may explain this.

2.5 CONCLUSIONS

Previous studies have suggested a strong negative impact of climate change on seabirds elsewhere in the North Atlantic (Table 2.4; Frederiksen et al., 2006; Osterblom et al., 2006); however the situation in the Celtic Sea appears to be much less clear.

Although previous works have demonstrated links between climatic conditions and seabird demographics in this region (Votier et al., 2005, 2008), these have mostly been connected with changes in NAO indices and are consistent with direct weather effects mediated by changes in storm frequency or wind conditions. Nevertheless, a recent study revealed a link between warmer waters in the Celtic Sea and offspring condition in Manx shearwater *Puffinus puffinus* (Riou et al., 2011). Therefore, the role of climate change on the Celtic Sea remains unclear but it certainly does not appear to share the same very strong signal exhibited elsewhere in the North Atlantic. Moreover, although kittiwake numbers have decreased significantly at Skomer in the past two decades, the numbers of the three Alcids have increased (Fig. 2.2). However, declines in the breeding success of these Alcids are perhaps reason for concern and this could be linked to density-dependent effects. In fact, breeding in large colonies seems to reduce predation on eggs or chicks; however, the competition for the best nesting sites can, in some cases, compromise the breeding success (Kokko et al., 2004). Therefore, we do not exclude that other factors such as predation (i.e. from gulls) probably play a role in the decline of Alcids productivity on Skomer.

Future research should focus upon multi-trophic level, region-wide research in order to understand the ecological processes regulating marine food webs in response to climate change. However, data availability is a common limitation in this approach and there are still only a small number of studies that have used these combined long-term datasets (representing all trophic levels from plankton to apex predators) in the North Atlantic (e.g. Aebischer et al., 1990; Hunt et al., 2002, Frederiksen et al., 2006). However we also urge that such ecosystem level approaches should also investigate the potential for synergistic effects of fisheries on climatic impacts. Marine ecosystems are not equally sensitive to

climate change, with some regions more vulnerable than others (Beaugrand et al., 2008). This study has important implications for our understanding of climate change impacts on marine ecosystems and in particular on apex predators, highlighting the importance of regional variability even within a relatively small geographic area (i.e. North Sea and Celtic Sea).

Table 2.4 Impact of climate variability across multiple trophic levels in the North Atlantic. SST: Sea Surface Temperature; NAO: North Atlantic Oscillation index.

Region	No. Trophic Levels examined	Groups	Climate predictor	Climate effect	Reference
North Sea	4	Seabird Pelagic fish Zooplankton Phytoplankton	SST	Negative (strong bottom-up)	Aebischer et al., 1990 Frederiksen et al., 2006
Newfoundland	2	Seabird Pelagic fish	SST	Negative	Carscadden et al., 2002
Baltic Sea	2	Seabird Pelagic fish	NAO	Negative	Österbloom et al., 2006
Gulf of Main	2	Seabird Pelagic fish	SST	Negative	Diamond and Devlin, 2003
Northern Norway	2	Seabird Pelagic fish	NAO, SST	Negative	Durant et al., 2003

Chapter 3

Regional variability and climate change effects in the pelagic food-web of three marine ecosystems around Great Britain

Abstract

Climate change has affected marine environments worldwide, leading to impacts on ecosystem structure and biodiversity. However, it is still unclear how these impacts affect ecological processes and the role of spatial variability, such that regional studies on climate change effect upon marine ecosystems are required.

The aim of this study was to investigate the spatial variability of climate change (bottom-up) effects in three marine ecosystems off southwest Britain: the Irish Sea, the Celtic Sea and the English Channel. Using long-term data (1991-2007), we modelled the pelagic food web across four trophic levels in each of these regions: phytoplankton, zooplankton, fish larvae and seabirds. We focussed upon the black-legged kittiwake (*Rissa tridactyla*), because they are widely distributed and previous work has shown regional variation in population size and productivity in response to changes in sea surface temperature (SST).

SST has increased in the North Atlantic over recent decades and has resulted in a change in marine environmental conditions, manifest as strong bottom-up effects in some regions (i.e. North Sea). Our results showed that the response to climate change across the three study regions was similar and much less pronounced than in the North Sea. We found only a weak bottom-up effect on mid-trophic level fish and kittiwakes in the Irish Sea food web; however while a significant relationship occurred between fish larvae and diatom abundance in the English Channel, this did not have any effect on

kittiwake productivity. No evidence for bottom-up effects was found in the Celtic Sea pelagic food web. We therefore speculate that changes in seabird numbers in these areas may be more strong influenced by other factors, such as differences in predation or fisheries impacts.

Our findings further highlight strong regional differences in multi-trophic level responses to climate variation in marine environments, supporting the hypothesis that the spatial effects of climate variability may vary across ecosystems and at small regional scales. Key to understanding these processes in more detail is to integrate other important stressors such as predation and fisheries.

3.1 INTRODUCTION

Climate change has affected marine environments worldwide leading to impacts on ecosystem structure and biodiversity. Human-induced climate change influences ecological processes and consequently the temporal and spatial patterns of species' distribution and abundance (Beaugrand et al., 2009). These effects operate through variation in climate influenced variables, such as sea surface temperature (SST), wind and currents. Responses to climate fluctuations are reflected in the productivity of marine ecosystems, from phytoplankton trought the dynamics of fish populations, and up to apex predators (Cushing, 1982; Sandvik et al., 2008).

An increase in temperature can influence regional vertical stratification of the water column and the associated nutrient availability (Carder et al., 1999; Sathyendranath et al., 2001), which may affect plankton productivity and distribution (Fromentin and Planque, 1996; Beaugrand et al., 2002; Richardson and Shoeman, 2004). Increasing SST has been shown to directly impact mid-trophic level fish, in particular affecting spawning and recruitment during the first year of life (Drinkwater and Myers, 1987;

Ottersen et al., 2004b). Typically, apex predators such as seabirds are more likely to be indirectly affected by increases in SST. This is normally manifest via bottom-up control, where changes in the availability of key prey (lower trophic levels; Schreiber, 2001) have had dramatic consequences upon seabird populations (Frederiksen et al., 2006). Despite some apparent patterns in the Northeast Atlantic (Richardson and Shoeman, 2004; McGyinty et al., 2011), and regional differences suggested at global scale (Brander, 2010; Overald et al., 2010), the extent of climate change effects upon marine systems is still unclear.

Marine ecosystems are not equally sensitive to climate change: in particular those at or near critical thermal boundaries are highly vulnerable to changing temperatures, which may lead to abrupt ecosystem shifts across multiple trophic levels (Beaugrand et al., 2008). Regional variability has been shown in the response of low trophic levels to rising SST in the Northeast Atlantic, with phytoplankton abundance increasing in cooler regions and decreasing in warmer regions (Richardson and Soeman, 2004). The regional response is often accompanied by structural changes in the zooplankton community (decline of cold temperate species) and by the geographical shift of species (Beaugrand et al., 2002). As well as low trophic levels, mid-trophic level fish reveal contrasting responses to climate change (Toresen and Østvedt 2000; Toresen 2001; Cardinale et al., 2004; Rijnsdorp et al., 2010). Understanding regional variation across the low and mid-trophic levels is a crucial step because of possible unexpected effects at the top of the food chain. In the North Sea, a bottom-up effect was found across four trophic levels, highlighting the key role of juvenile fish stages (fish larvae) in the pelagic food web and their importance for seabirds (Frederiksen et al., 2006). These findings emphasized the necessity of identifying regional variation in response to climate change at multiple trophic-levels, as well as the ecological role of fish larvae for apex predators in other areas around Great Britain.

The aim of this study was to test for climate-related influences and regional variability across four trophic levels in each of three marine regions off southwest Britain: the Irish Sea, the Celtic Sea and the English Channel, focussing in particular on one apex predator species the black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake). These regions are each productive ecosystems in the northeast Atlantic, supporting large communities of apex predators including internationally important numbers of seabirds (Mitchell et al., 2004). The kittiwake is one of the most widely distributed and numerous seabird species across the British Isles (8% of the world's kittiwake population breed around Great Britain (Mitchell et al., 2004), even though numbers have declined considerably in recent decades (by 25% in the UK between the 1985-88 and 1998-2002 surveys; JNCC, 2012), at least partly in response to climate mediated changes in prey availability (Frederiken et al., 2004, 2007). Kittiwakes have been highlighted as reliable and sensitive indicators of marine ecosystem functioning: they are surface feeders with a short foraging range of approximately 35km during the breeding season, relative small size, high foraging cost, and a specialist diet (Furness and Tasker, 2000; Dierschke et al., 2004).

Long-term data on kittiwake numbers and breeding success have been collected throughout Britain and Ireland since 1986 (Mavor et al., 2003). Kittiwake numbers around the British Isles have declined, in particular around the North Sea coast by about 50% since the mid- 1980s, responding to a decline in their main prey, lesser sandeel (*Ammodytes marinus*, hereafter sandeel; Wanless et al., 2007). By contrast, kittiwake populations are quite stable in Wales, although a slight decrease in their abundance has been recorded in recent years (JNCC, 2012), the reasons for which are not well understood. In the southwest of Great Britain, kittiwake populations have not remained stable and there has been a decline in numbers, including the abandonment of several colonies in the coastal counties of southern England in recent decades (Brown et al., in

prep). This decline is ongoing, making an enhanced understanding of the key mechanisms driving decline urgent. Kittiwake colonies in the British Isles tend to form geographical clusters sharing similar patterns of annual fluctuations in breeding success (Furness et al., 1996). This spatial variation indicates that the factors responsible differ between regions, and the great between-year variance observed in kittiwake breeding success (Furness et al., 1996; Frederiksen et al., 2007a; Wanless et al., 2007) suggests that this species' productivity is likely to respond to small scale processes, for example changes in food availability (i.e. sandeel abundance; Frederiksen et al., 2005), highlighting the necessity to conduct more research at different regional scales.

3.2 MATERIALS AND METHODS

Defining the regional ecosystems

The study area considered here is a part of the Northeast Atlantic continental shelf, southwest of the United Kingdom. The main oceanographic feature in this area is the presence of frontal systems, such as the Irish Shelf Front that occurs to the south and west of Ireland, and exists all year-round. This front marks the boundary between waters of the shelf (often mixed vertically by the tide) and offshore North Atlantic waters. The turbulence caused by the front introduces nutrients from deeper waters to the surface, where they promote the growth of phytoplankton, especially diatoms in spring (OSPAR, 2002).

This part of the continental shelf can be sub-divided into three regions identified as the Irish Sea, Celtic Sea and the English Channel (Fig 3.1a). These were identified on the basis of the presence of seasonal front systems which tend to develop during spring: the Celtic Sea front (dividing the Celtic Sea from the Irish Sea); and the Ushant Front (which develops from the coast of Brittany and extends to the western English Channel,

dividing the Celtic Sea from the English Channel; ICES, 2007; Fig. 3.1a). The Celtic Sea front tends to develop in late spring at the confluence of cooler mixed waters from the St. George's Channel and the warmer stratified waters of the Celtic Sea (OSPAR, 2002), while the Ushant front is a seasonal tidal frontal system (Videau, 1987) which separates the vertical mixed waters of the English Channel from the stratified waters of the Celtic Sea in spring (Holligan et al., 1984). Frontal systems are transition zones and often effective barriers between very different ecosystems/water masses with different physical proprieties and nutrient availability (Durant et al., 2004). These represent changes associated with nutrient availability from deeper nutrient-rich waters supporting all members of the food web (Durant et al., 2004). Fronts are regions of enhanced plankton production (Pingree et al., 1976; Holligan, 1981), leading to higher fish production (Mann and Lazier, 1996), and consequently act to concentrate prey for apex predators such as sharks and seabirds (Schneider, 1990; Hunt, 1990; Priede and Miller, 2009).

Biotic and abiotic variables selection

In each region of our study area, long-term data from 1986 to 2007 for four trophic levels (phytoplankton, zooplankton, fish larvae and seabird) were collated and analysed along with local-scale measures of SST (winter SST and annual SST). Regional measures of SST were preferred to a large scale climate variability indicator (such as North Atlantic Oscillation Index) as more suitable proxies of local climate effects on marine systems (Frederiksen et al., 2004b). While SSTs have increased everywhere in the northeast Atlantic in recent years, a marked regional variation is apparent, with more rapid increases in the North Sea than west of the British Isles (Edwards et al., 2006).

Our covariates were chosen according to the following criteria: average measures of diatom abundance (spring: March-June), copepod biomass (*Calanus* spp.), fish larval abundance, and a measure of kittiwake productivity (breeding success). These were

used to investigate long-term trends. In addition, we tested for direct and indirect effects of climate across four trophic levels. Direct effects were expected via a significant correlation between abundance/biomass/productivity and SST (winter SST) for plankton and fish. Indirect effects were expected via bottom-up processes, characterised by a positive correlation between a measure of predator abundance/biomass/demography and prey abundance/biomass. Diatom abundance was used as a food proxy for copepods, while diatom abundance and copepod biomass were used as a food proxy for juvenile fish (fish larvae) (Frederiksen et al., 2006). Kittiwakes were assumed to feed upon 1 and 0-year fish larvae (Wanless et al., 2007). An indirect climate effect on seabirds was expected via a significant correlation with lagged annual SST (1-year lag).

Plankton data: the Continuous Plankton Recorder (CPR)

The Continuous Plankton Recorder (CPR) survey is a plankton monitoring programme that has been operated on a routine monthly basis since 1931 (see Richardson et al., 2006). The CPR survey is recognised as one of the longest, richest (in terms of species information) and geographically extensive ecological surveys in the world. These data have been used numerous times in ecological studies (e.g. Richardson and Shoeman, 2004; Frederiksen et al., 2006).

A total of 2145 CPR samples, taken between 1991 and 2007, were considered in the analysis to investigate possible changes in the plankton community in the Irish Sea (52ºN-55º, 7ºE-2ºW), Celtic Sea (50ºN-52º, 10ºE-5ºW) and English Channel (49ºN-51º, 10ºE-1ºW) (Fig. 3.1b). The abundance of diatoms and copepods was determined in each sample and annual means calculated by averaging across samples taken in the period March-June. Calanoid copepod (total length >2mm) biomass was calculated by multiplying the abundance of each copepod species by its average mass estimated from an allometric relationship based on size (Richardson et al., 2006). Diatom abundance

was used as a proxy for copepod food availability (Frederiksen et al., 2006). Pelagic marine fish larvae feed upon nauplii and copepods (Hunter et al., 1980); however because information on nauplii abundance was not available we used both diatom abundance (which is a food proxy for nauplii) and copepod biomass as a proxy for fish larvae food (Frederiksen et al., 2006).

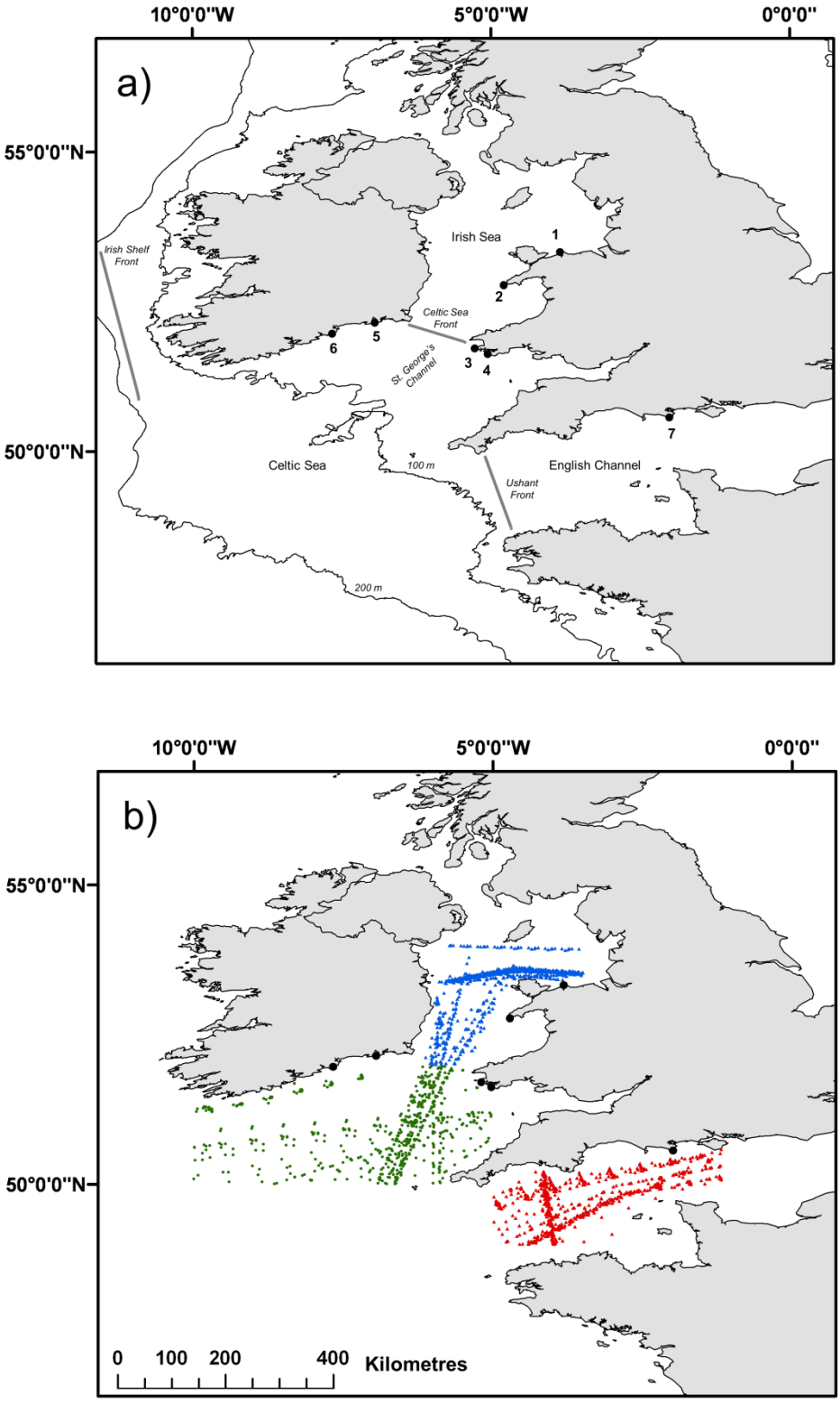

Figure 3.1 (a) Map of the study area, including frontal systems (adapted from OSPAR, 2004). The locations of kittiwake (*Rissa tridactyla*) colonies investigated in this study are also presented; 1: Great Ormes Head (53° 20N, 3° 51W), 2: Bardsey Island (52° 72N, 4° 77′W), 3: Skomer Island (51° 40N, 05° 15W), 4: Elegug Stacks (51° 60N, 04° 98W), 5: Dunmore East (51° 15N, 06° 99W), 6: Ram Head (51° 15N, 07° 70W), 7: Durlston Head (50° 54N, 02° 02W). (b) Map of the study area, showing the locations of all CPR samples for the three regions from March to June. In blues samples used for the Irish Sea (52°N-55°, 7°E-2°W) spanning from 1991-2007, in green samples used for the Celtic Sea (50°N-52°, 10°E-5°W) spanning from 1991-2007, in red sample used for the English Channel (49°N-51°, 10°E-1°W) spanning from 1991-2004.

Fish larvae

Long term abundance estimates derived from stock assessments (e.g. ICES) on small pelagic fish (sandeel, sprat *Sprattus sprattus* and herring *Clupea harengus*) either did not exist, or were not consistent for all three regions which form the study area (e.g. herring is assessed in the Irish Sea and Celtic Sea, but there is no assessment in the English Channel). For this reason we decided to use fish larvae estimates derived from the CPR which were available for the entire study area. Fish larval abundance of Clupeidae and Ammodytidae were extracted from the CPR and averaged for the period March-June. Previous studies have utilized CPR fish larvae data (abundance and length) to obtain a biomass index of sandeel for the North Sea (Frederiksen et al., 2006); however this was not possible in our case as information for fish larvae lengths was not available. Fish larval abundance for the current and previous year was used as a proxy for food availability for kittiwakes, and assumed to affect seabird productivity via resource limitation.

Seabirds

Data on kittiwake breeding success were collated (Joint Nature Conservation Committee, JNCC - jncc.gov.uk/seabirds) for seven breeding colonies in the southwest of Great Britain (Fig. 3.1a): two in the Irish Sea (Great Ormes Head 53° 20N, 3° 51W; and Bardsey Island 52° 72N, 4° 77′W); four in the Celtic Sea (Skomer 51º 40N, 05º 15W; Elegug Stacks 51º 60N, 04º 98W; Dunmore East 51º 15N, 06º 99W; and Ram Head 51º 15N, 07º 70W) and one in the English Channel (Durlston Head 50º 54N, 02º 02W). In order to compare variation in productivity among the colonies, data spanning the period from 1991 to 2007 were selected, with the exception of the colony in the English Channel where data after 2004 were not available (Fig. 3.2 m-p).

Environmental variables

In this study both winter SST (WSST, December-March) and annual average SST (1-year lag) were used as climate predictors for each region. Winter SST was used to test for direct effects on plankton and fish larvae. As the recruitment probability for pelagic fish varies with temperature change, in particular during their first years of life (Ottersen and Stenseth, 2001), a broader index (annual SST, 1-year lag) was used to test the indirect climate effect on seabirds (kittiwake). Monthly SST data from 1991 to 2007 were derived from satellite images and collated from the POET database available at http://poet.jpl.nasa.gov with a spatial resolution of 0.04º longitude x 0.04º latitude (Fig. 3.2 a-c).

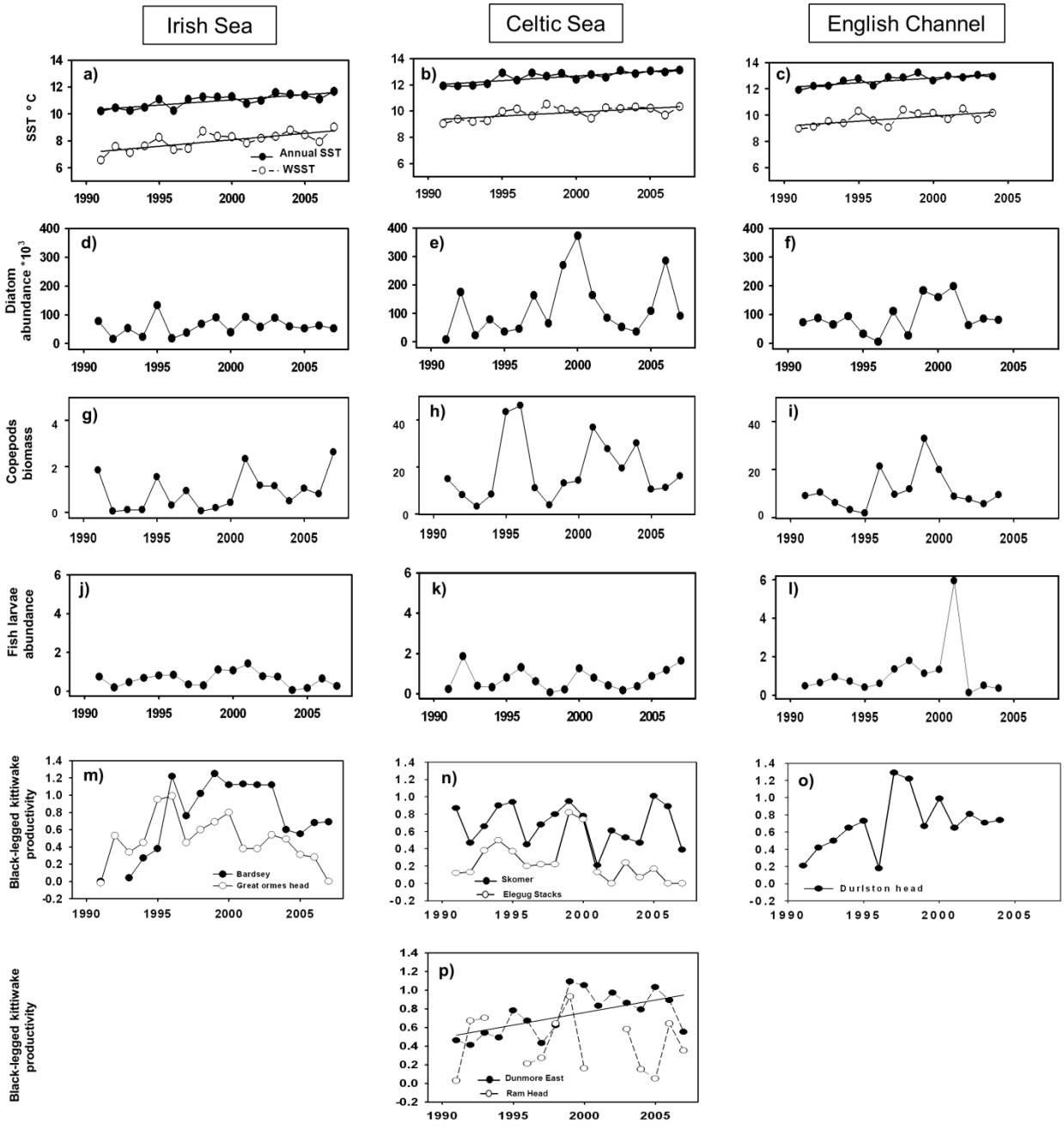

Figure 3.2 Variables used for the models construction for each region: Sea Surface Temperature (ºC) (a-c); Diatom abundance (d-f); copepods biomass (mg wet weight) (g-i); fish larval abundance (j-l); Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size) (m-p). The line indicates when temporal trends are present. Note the scales differ.

Model construction and statistical analyses

For each region correlations among explanatory variables were tested before model development. In order to investigate the difference between regions both explanatory and response variables were also tested for correlation.

We tested successively for possible temporal trends in our data using linear regression. Multiple regression models were used to identify the main predictors (environmental conditions, food availability) for each trophic level (diatoms, copepods, fish larvae and seabirds). When the dependent variable was not normally distributed, it was log (base 10) transformed. Kittiwake productivity (breeding success) was expressed as the number of fledged chicks per breeding pair per year, weighted by the number of pairs sampled.

Starting from the full model, the most parsimonious model for each trophic level was selected on the basis of the lowest Akaike Information Criterion (AIC), corrected for small sample size (AIC_c). In order to evaluate the robustness of the significant relationships in the best model, a number of single-variable models were run to examine the effects of explanatory variables in the absence of others. The variables used for the model construction are shown in Table 3.1.

A set of candidate models was compared using differences in AIC_c between the top-ranked and current model (delta AIC_c), and by calculating the AIC_c weight (the scaled likelihood that each model is the best description of the data, Burnham and Anderson. 2002). Competing models were selected when having their AIC_c within 2 of the lowest, as they were considered to have equivalent support from the data (Burnham and Anderson 1998) and are presented in Appendix 2, Table A 2.4-2.5. Model goodness of fit was compared using the deviance and coefficient of determination (R^2). Covariates were considered statistically significant when the *p* value was <0.05. Model residuals

were evaluated to check for non-normality, heteroscedasticity and autocorrelation of errors. All modelling was carried out using R version 2.14.1 (R Development Core Team, 2011).

Table 3.1 Response variables and predictors used for the multiple regression models. For each response variable the full model is also given. WSST: Winter Sea Surface Temperature; 1Lag-SST: 1 year lagged annual Sea Surface Temperature; Kittiwake BS: Breeding Success expressed as the number of fledged chicks per breeding pair per year, weighted for sample size.

Response Variable	**Climate effect**	**Food availability**	**Full model**
Diatom abundance	WSST		Diatom ~ WSST + year
Copepods biomass	WSST	Diatom	Copepods ~ WSST + diatom + year
Fish larval abundance	WSST	Diatom; Copepods	Fish larvae~ WSST + diatom + copepods + year
Kittiwake BS	1Lag-SST	Fish larvae Fish larvae lag	Kittiwake ~ 1Lag-SST+ fish larvae + 1lag-fish larvae + year

3.3 RESULTS

Correlation between covariates

Preliminary explanatory analyses for each region showed that correlation occurred in some cases (Appendix 2, Table A2.1-2.3). In particular winter SST and annual SST were significantly positively correlated with each other in all the regions (Irish Sea: r = 0.89, p <0.001; Celtic Sea: r = 0.68, p <0.001; and English Channel: r = 0.57, p = 0.03), and with year (Irish Sea: WSST: r = 0.75, p <0.001; annual SST: r = 0.81, p <0.001; Celtic Sea: WSST: r = 0.65, p = 0.004; annual SST: r = 0.81, p <0.001; English Channel: WSST: r = 0.61, p = 0.02; annual SST: r = 0.79, p <0.001).

Between region correlation occurred only for some of the covariates (Appendix 2. Table A2.4). In particular significant positive correlations (p <0.001) were found in both SST measures (winter SST and annual SST) between the different regions. Diatom abundance in the English Channel was significantly correlated with the abundance in the Celtic sea (r = 0.65, p = 0.011), but none of these measures was significantly correlated with diatoms in the Irish Sea (Table A2.4).

Environmental variables

Temporal trends occurred in both environmental variables (WSST, annual SST), and are shown in Fig. 3.2a-c. Sea surface temperature increased significantly over time in all the regions (Irish Sea WSST: p <0.001, slope = 0.095±0.022; annual SST: p <0.001, slope = 0.077±0.014; Celtic Sea WSST: p = 0.004, slope = 0.059±0.017; annual SST: p <0.001, slope = 0.070±0.012; and English Channel WSST: p <0.02, slope = 0.075±0.028; annual SST: p <0.001, slope = 0.073±0.016). The Irish Sea waters were cooler than the other two regions with a temperature average of 7.99º C for WSST, 10.97º C for annual SST. By contrast, in the Celtic Sea and English Channel SST averages were similar (Celtic Sea: 9.86º C WSST and 12.61º C annual SST; English Channel 9.72º C WSST and 12.63º C annual SST).

Phytoplankton

Diatom abundance fluctuated over time in all regions, with no clear linear trend (Fig. 3.2d-f). Diatom variability was not explained by SST in any of the regions Our most parsimonious model included the intercept only for the Irish Sea and English Channel (Table 3.2 and 3.4); for the Celtic Sea the best model selected for diatom included only year, although this was still not statistically significant with an alpha level of 5% (p = 0.09).

Zooplankton

Copepod biomass fluctuated over time in all three regions, with no clear linear trend (Fig. 3.2g-i). In the Irish Sea our most parsimonious model explaining changes in copepod biomass included diatom abundance, although this was not statistically significant at the alpha level of 5% (Table 3.2). In the Celtic Sea and English Channel our most parsimonious model included the intercept only (Table 3.3-3.4).

Fish larvae

Fish larval abundance fluctuated over time, with no clear trend (Fig. 3.2j-l). Climate effect (WSST) or food availability (i.e. diatom and copepods) did not explain variation in fish larval abundance in the Irish Sea. Our most parsimonious model included the intercept only (Table 3.2). Similarly, no climate effect was found in the Celtic Sea; however the best model selected included only diatoms, although no significant relationship was found (p = 0.09) (Table 3.3). In the English Channel, a very weak positive significant relationship was found with diatom abundance (p = 0.04, slope = $0.395x10^{-7}\pm0.171x10^{-7}$), but there was no evidence for an effect of SST (Table 3.4).

Seabirds

Kittiwakes showed highly variable reproductive success in both colonies in the Irish Sea; however there was no significant correlation between the two over the study period (ρ =

0.35, p = 0.18). Kittiwake productivity at Bardsey increased during the first half of study period (1991-1999, Fig. 3.2m), ranging from 0 chicks pair^{-1} in 1991 to 0.69 chicks pair^{-1} in 2007 with a maximum of 1.25 chicks pair^{-1} in 1999. It was significantly positively correlated with fish larvae (p = 0.02, slope = 0.604±0.233), and year (p = 0.02, slope = 0.048±0.017) (Table 3.2). Kittiwake productivity at Great Ormes Head declined from 1996 (Fig. 3.2m), and did not appear to be regulated by our measures of food availability (i.e. fish larval abundance during the current and previous year) or SST. Our most parsimonious model included the intercept only (Table 3.2).

In the Celtic Sea, kittiwakes showed highly variable reproductive success between colonies, with productivity of close colonies better correlated (Skomer and Elegug Stack) (r = 0.44, p = 0.07). Kittiwake productivity at Skomer ranged from 0.21 chicks pair^{-1} in 2001 to 1.01 chicks pair^{-1} in 2005 (Fig. 3.2n), but was not significantly correlated with any covariates (Table 3.3). Kittiwake's at Elegug Stack produced a maximum of 0.82 chicks pair^{-1} in 1999, while there was complete reproductive failure (0 chicks pair^{-1}) in 2002, 2006 and 2007 (Fig. 3.2n). Our most parsimonious model included the intercept only (Table 3.3). Kittiwake productivity at Dunmore East increased over time (p = 0.012, slope = 0.026±0.009) with a maximum of 1.09 chicks pair^{-1} in 1999 (Fig. 3.2p), but was not significantly correlated with any covariates (Table 3.3). Kittiwake's at Ram Head showed a variable productivity with a peak in 1999 (0.93 chicks pair^{-1}) (Fig. 3.2p). Our most parsimonious model included the intercept only (Table 3.3).

In the English Channel kittiwake reproductive success increased over time at Durlston Head (Fig. 3.2o) ranging from 0.21 chicks pair^{-1} in 1991 to 0.74 chicks pair^{-1} in 2004, but this increase was not statistically significant. Neither SST (annual SST lagged by 1year) nor food availability (fish larval abundance during the current and previous year)

(Table 3.4) explained variation in kittiwake productivity, with the most parsimonious model including the intercept only (Table 3.4).

Table 3.2 Model selection to estimate factors influencing each trophic level for the Irish Sea. Only the best supported models are shown. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: adjusted coefficient. Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS							
Diatom abundance							
Intercept only	0.47	1	17	1.04		<0.001	4.717 (±0.06)
PRIMARY CONSUMERS							
Copepod biomass							
diatom	0.31	2	17	8.14	0.16	0.062	$0.121x10^{-6}$($\pm 6.05 x10^{-6}$)
Fish larval abundance							
Intercept only	0.26	1	17	2.29		<0.001	0.626 (±0.091)
APEX PREDATORS							
Black-legged kittiwake productivity							
Bardsey							
fish larvae + year	0.28	3	16	1.39	0.38	**fish larvae 0.022** **year 0.018**	0.604 (±0.233) 0.048 (±0.0.17)
Great Ormes Head							
Intercept only	0.20	1	17	1.00		<0.001	0.500 (±0.060)

Table 3.3 Model selection to estimate factors influencing each trophic level for the Celtic Sea. Only the best supported models are shown. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: adjusted coefficient. Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS							
Diatom abundance							
year	0.42	2	17	2.45	0.12	0.098	0.035 (±0.020)
PRIMARY CONSUMERS							
Copepod biomass							
Intercept only	0.44	1	17	1.83			1.115 (±0.082)
Fish larval abundance							
diatom	0.29	2	17	3.93	0.12	0.097	0.526 (±0.297)
APEX PREDATORS							
Black-legged kittiwake productivity							
Skomer							
Intercept only	0.24	1	17	0.88		<0.001	0.682 (±0.056)
Elegug Stacks							
Intercept only	0.20	1	17	0.096		<0.001	0.091 (±0.018)
Dunmore East							
fish larvae lag + year	0.38	3	17	0.434	0.41	fish larvae lag 0.07 **year 0.008**	-0.172 (±0.089) 0.026 (±0.008)
Ram Head							
Intercept only	0.35	1	13	0.860		<0.001	0.442 (±0.074)

Table 3.4 Model selection to estimate factors influencing each trophic level for the English Channel. Only the best supported models are shown. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: adjusted coefficient. Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS							
Diatom abundance							
Intercept only	0.59	1	14	2.18	0.12	<0.001	4.834 (±0.109)
PRIMARY CONSUMERS							
Copepod biomass							
Intercept only	0.48	1	14	1.38		<0.001	0.942 (±0.087)
Fish larval abundance							
diatom	0.43	2	14	1.48	0.25	**0.039**	0.395×10^{-7} ($\pm 0.171 \times 10^{-7}$)
APEX PREDATORS							
Black-legged kittiwake productivity							
Durlston Head							
Intercept only	0.28	1	14	1.35		<0.001	0.697 (±0.086)

3.4 DISCUSSION

Our results showed that the response to climate change across three regions (Irish Sea, Celtic Sea and English Channel) in Great Britain is broadly similar and, despite changing environmental conditions in the three regions (i.e. increasing SST), there is no evidence of a bottom-up signal across four trophic levels. There was little evidence of the patterns expected if regulation through local food availability was the dominant process from primary consumers, through to kittiwakes. There was, however, a significant positive correlation between kittiwake breeding success and fish larval abundance at one Irish Sea colony (Bardsey), indicating small-scale regional differences in factors affecting seabird (kittiwake) demographics during the study period. A significant relationship was evident between fish larval abundance and diatom abundance in the English Channel, but this did not appear to have an effect on seabirds. In addition, the Celtic Sea food web did not seem to be influenced by bottom-up processes. Despite these differences, we suggest that there is not a strong effect of spatial variability between the three regions. Possible explanations for these findings, as well as comparisons with climate related patterns in other regions, are discussed below.

Regional response to direct climate change effects

Richardson and Schoeman (2004) showed an increase in phytoplankton abundance between 1958 and 2002 in the cooler regions of the Northeast Atlantic (north of 55°N) and a decrease in warmer regions (south of 50°N) in response to climate warming. It has been suggested that these different responses are likely to be dependent upon changes in water vertical mixing and nutrient availability. In the North Sea, phytoplankton biomass increased during the mid-1980s in response to increasing SST (Beaugrand and Reid, 2003). Our results differ from these previous findings, and despite the year-to-year (1991-2007) fluctuations in diatom abundance in the Irish Sea, Celtic Sea and English Channel (Fig. 3.2d-f), this was not directly linked with changes in winter SST. This

contrasting response of primary producers in the southwest of Great Britain may be linked to different oceanographic conditions. For example, both the Irish Sea and western English Channel waters are mixed during the summer (Holligan et al., 1984; OSPAR, 2002), which may explain why there is not a linear trend in diatom abundance despite the increase in SST. This contrasts with the Celtic Sea, which is stratified during the summer (OSPAR, 2002), where diatom abundance has increased over the study period (Fig. 3.2e).

Our findings suggest that zooplankton biomass (calanoid copepod) is also not influenced by changes in winter SST in the southwest of Great Britain (Table 3.2-3.4). This is in contrast with the North Sea where abundance of pseudo-temperate calanoid copepod species (e.g. *Calanus helgolandicus*) is positively correlated with SST (Beaugrand et al., 2002). Despite the suggestion of regional differences across the Northeast Atlantic (McGinty et al., 2011), there does not appear to be such variation at this smaller scale. The lack of a strong climate signal in copepod biomass (Table 3.2-3.4) over the period 1991-2007 in our study indicates that either these changes are not apparent in recent decades, or that longer term studies (over four decades) are necessary to explain the relationship between climate and plankton. Another possible explanation could be that the southwest ecosystems (Irish Sea, Celtic Sea and English Channel) are not in critical thermal boundaries respect to other regions (North Sea) in the Northeast Atlantic (Beaugrand et al., 2008), and for this reason are more resilient to climate change impact.

The abundace of fish larvae (sandeel and clupeids) varied between years in all regions (Fig. 3.2j-l) showing uncorrelated patterns (Table A2.4). Therefore, our results did not indicate a climate effect (winter SST) (Table 3.2-3.4). This is in contrast with previous findings in the Northeast Atlantic where a negative effect of SST was found on fish abundance (Arnott and Ruxton, 2002). Our results suggest that, as general pattern,

climate change does not seem to influence fish larvae in the southwest of Great Britain; however, we cannot exclude that this apparent absence of signal may actually be related to data limitations.

Regional patterns and trophic coupling across four trophic levels

Our results suggest that during 1991-2007, the Irish Sea, Celtic Sea and English Channel were not strongly regulated via bottom-up forcing (Table 3.2-3.4). At low trophic levels, some regional differences emerged with some trophic coupling between fish larvae and diatoms in the English Channel, but no significant relationship was found for the Irish Sea and Celtic Sea. Given the strong increase in SST over this period in all the regions (Fig. 3.2a-c; Edwards et al., 2006), we had predicted bottom-up control; however these results suggest that strong regional variability does not occur in the southwest of Great Britain.

At the highest trophic levels, our results have shown that in the Celtic Sea and English Channel kittiwake colonies are not influenced by food availability (Table 3.3-3.4). A different situation was found for one of the colonies in the Irish Sea, however, where a positive relationship between kittiwake productivity and fish larval abundance occurred at Bardsey Colony in the Irish Sea (Table 3.2). These regional differences may be due to a positive effect of increasing SST on pelagic fish in the Irish Sea. In this region, sea temperature is cooler than the Celtic Sea and English Channel which have a similar SST range; however the ecological mechanism involved remains unclear. The lack of relationship between kittiwake productivity and prey availability in the Celtic Sea suggests that perhaps other ecological mechanisms (i.e. predation, fisheries) may influence kittiwake breeding success in this region. Our results suggest that kittiwake productivity is not controlled by changes in prey availability in the English Channel. However, we do not exclude the fact that in this particular case only data for one colony was available and a different situation might occur in other colonies in this region.

Frederiksen et al. (2005) suggested that patchiness and non-synchronous dynamics of prey populations, in response to spatio-temporal variation in the physical environment, would lead to regional variation in kittiwake breeding success. Within regions, however, changes in prey availability or disturbance effects (i.e. density-dependence, predation) could have differential impacts on population dynamics. Our results showed that kittiwake productivity in two neighbouring colonies in the Irish Sea (Bardsey and Great Ormes Head) responded differently to changes in prey availability (Table 3.2). In particular, the recent decline at Great Ormes Head is not determined by bottom-up effects. Therefore the Celtic Sea colonies showed similar trends, which was not explained by resources limitation, suggesting that in this case the local scale factors influencing kittiwake productivity might be similar. Regional studies across multiple trophic levels may constitute a valuable approach in informing seabird conservation policy and more research should focus on this type of approach.

3.5 CONCLUSIONS AND RECOMENDATIONS

This study helps clarify the response of different marine ecosystems around the British Isles to climate variation, in particular focussing upon an important seabird species. Previous studies have suggested a strong negative impact of climate change on seabirds in the Northeast Atlantic (Carscadden et al., 2002; Ostebloom et al., 2006), and in particular in the North Sea (Aebischer et al., 1990; Frederiksen et al., 2006). The lack of strong bottom-up effect in the Irish Sea, Celtic Sea and English Channel pelagic food webs, however, supports the hypothesis that the spatial effect of climate change varies across ecosystems and at small regional scales. Beaugrand et al. (2008) showed that regions in which regime shift has occurred (i.e. North Sea) appear to be the most vulnerable to climate change impacts in the North Atlantic, while other areas can remain relatively ecologically stable over long periods. From our results, it seems most likely

that the marine ecosystems in the southwest of Great Britain have not yet experienced a regime shift, or that this has occurred before the study period. Ecological studies should focus upon the application of a multiple trophic level approach at different geographical scales to include all important information. Recent studies have included regional variability while researching the climate change effect upon some components of the food web (Frederiksen et al., 2005, 2007a; Beaugrand et al., 2009; McGinty et al., 2011); however further investigations at a more complex level are needed in order to obtain a comprehensive description of the possible ecological mechanisms involved in the study of the effects of climate change on marine ecosystems. While data availability is a common limitation in multiple trophic level studies and appropriate caveats need to be considered when extrapolating inferences from regional studies, this study has important implications for our understanding of climate change impacts on marine ecosystems and in particular on apex predators, highlighting the importance of regional variability.

Chapter 4

Trophic relationships of seabirds in the Celtic Sea ecosystem: a view from an ECOPATH model

Abstract

Apex predators such as seabirds play an important functional role in marine ecosystems. Seabirds may affect the trophic dynamics and diversity of the ecosystems in which they occur in response to fisheries impacts (top-down), or they may be influenced by changes at the base of the food web (bottom-up). Understanding these trophic relationships and their structural role can be useful in predicting the response of seabirds to fishing and climate variability and the effects of those responses on other ecosystem components.

The Celtic Sea is a productive shelf region of the Northeast Atlantic, and an important area for seabird conservation. An Ecopath model was constructed to quantitatively describe the trophic role of seabirds in this region. The analysis of the trophic structure of the Celtic Sea showed that it is a mature ecosystem in terms of species richness, number of trophic interactions and detritus recycling rates (*sensu* Odum). Our results show that six seabird functional groups respond to biomass changes of primary producers and consumers, as well as mid-trophic level fish (schooling pelagic fish such as sprat *Sprattus sprattus* and herring *Clupea harengus*). In addition, changes in the biomass of other pelagic fish species such as mackerel *Scomber scombrus* (L.) and garfish *Belone belone* (L.) may influence seabird biomass in the Celtic Sea. Seabirds are also vulnerable to the impact of fisheries and our results reveal that the biomass of scavenger species (such as surface feeders and gulls) increases with the amount of discards in the system; the increase in gull biomass has an indirect negative effect on the

biomass of other seabirds (inshore and offshore divers) in response to predation pressure from gulls. This study represents the first application of such a complex trophic model to the Celtic Sea, and its results contribute significantly to our understanding of the organization and trophic transfers between biological groups within this ecosystem. Our findings can be used to support management schemes for seabird conservation and provide an ecosystem based approach for fisheries.

4.1 INTRODUCTION

In recent decades human activities such as overfishing (Pauly, 1998), climate change (Ottersen et al., 2001), and pollution (Votier et al., 2005) have substantially affected the marine environment. Future alarming predictions suggest that these impacts are likely to influence the functioning of marine ecosystems (i.e. biodiversity, community assemblage, trophic links; Stockstad, 2006). Under this scenario, understanding marine system functioning is essential for sustainable marine resource management and conservation.

Due to the complex structure of marine ecosystems, an impact on one component of the food web (e.g. top predator or primary producer) can have dramatic and potentially unforeseen effects on another component via trophic linkage (Daskalov et al., 2007). Human-induced impacts, such as fishing or anthropogenic-driven climate change, have been shown to have profound consequences among multiple trophic levels (Frederiksen et al., 2004a). Fisheries, by removing large top-predators (top-down control), may generate trophic cascades (Osterbloom et al., 2007), or in some cases compete with apex predators for resources (Furness, 2003). In addition, fishing can alter the structure of the marine ecosystem (e.g. by reducing the mean trophic level, Pinnegar et al., 2002). Climate change may influence overall productivity of marine ecosystems by changing

the distribution and composition of plankton communities via a bottom-up effect (Beaugrand, 2005; Conversi et al., 2010), which can alter the distribution and abundance of mid-trophic level fish that provide a key link to top predators (Mavor et al., 2005). Finally, there is also evidence that fisheries exploitation and climate variability may have synergistic impacts on marine ecosystems (Planque et al., 2010).

The application of an ecosystem-based approach has become widely recognised as an important resource management tool in the light of these changes (Link, 2002; Garcia et al., 2003), partly because of its ability to recreate complex trophic dynamics (Fulton, 2010) that are a feature of so many marine ecosystems, but also to isolate species interactions (e.g. predator-prey relationship) in response to the effects of fisheries and climate change (Fulton and Smith, 2004). In recent years, the study of marine ecosystems has evolved from single and multiple-species models to more complex ecosystem-based approaches (FAO, 2003). The application of such models has become widespread, in particular tropho-dynamic models such as Ecopath with Ecosim (Christensen et al., 2004; Plaganyi, 2007). This popular approach has been widely applied for constructing food web models (Pauly et al., 2000) and, despite its limitations (Plagányi and Butterworth 2004), this software has been used worldwide for addressing ecological questions and for fisheries policy exploration (Christensen and Walters, 2004).

Incorporating apex predators, such as seabirds, into large-scale ecosystem-based model approaches has been acknowledged as an integral part of understanding food web structure and ecosystem functions (Cairns, 1992; Fowler, 1999), however relatively few studies have specifically used this technique with respect to seabirds (Aebischer et al., 1990; Frederiksen et al., 2006; Hunt et al., 2002; Luckzac et al., 2011). Seabirds are key species in marine ecosystems (Weimerskirch et al., 2003), and their response to changes in prey availability can also be used to gain information on the state of fish stocks, or to

understand the impacts of environmental change (Barrett and Krasnow, 1996; Kitaysky et al., 2000). Previous studies have tried to examine the response of seabirds to climate variation and fishery impacts in other regions in the North Atlantic (i.e. North Sea) by using multi-trophic level approaches (Aebischer, 1990; Frederiksen et al., 2006), but our understanding of the ecological role of apex predators is often hindered by lack of information on their trophic ecology (Matich et al., 2011).

The Celtic Sea is a particularly important region in terms of fish and invertebrate biodiversity (Ellis et al., 2002) with high seabird and marine mammal species richness (Mitchel et al., 2004; Hammond et al., 2006). This region also supports several important European fisheries (Pinnegar et al., 2002), which in recent years have been shown to have negative effects upon ecosystem structure (Pinnegar et al., 2002; Blanchard et al., 2005) in the Celtic Sea, underlining the importance of formulating a solid management plan to aid its protection.

However, very little is known about the structure and functioning of the Celtic Sea food web, and its possible response to fisheries impacts. The aim of the present study is to describe the trophic linkages in the Celtic Sea ecosystem, focusing on the functional role of apex predators (seabirds) by using the complex ecosystem-based model Ecopath with Ecosim (EwE). The results of this study can be used as a basis for support for further study directed at the production of an ecosystem-based management plan for this region.

4.2 MATERIALS AND METHODS

The study area

The Celtic Sea is an area of continental shelf situated to the southwest of Great Britain, which corresponds to ICES divisions VIIf-j considered in this study (Fig. 4.1). The region differs in its fish assemblages and its physical characteristics (ocean circulation, system fronts) from neighbouring regions such as the Irish Sea, English Channel and the Bay of Biscay (Trenkel et al., 2004; OSPAR, 2002). The Celtic Sea also supports a large multi-national fishing fleet with vessels from France, Ireland, UK, Spain and Belgium, which produces large quantities of discards (Enever et al., 2007). The fishery mainly targets pelagic species (e.g. mackerel, *Scomber scombrus* and horse mackerel, *Trachurus trachurus* (L.); Eaton, 1983; Lockwood and Shepherd, 1984)) probably in response to the decline of traditionally exploited species (i.e. cod, *Gadus morhua* (L.)) (Pinnegar et al., 2002). These changes in the structure of the fish community are reflected in the size of landed fish, where, in addition to a decrease in the abundance of larger fish, there has been a concomitant increase in the abundance of smaller fish (Blanchard et al., 2005).

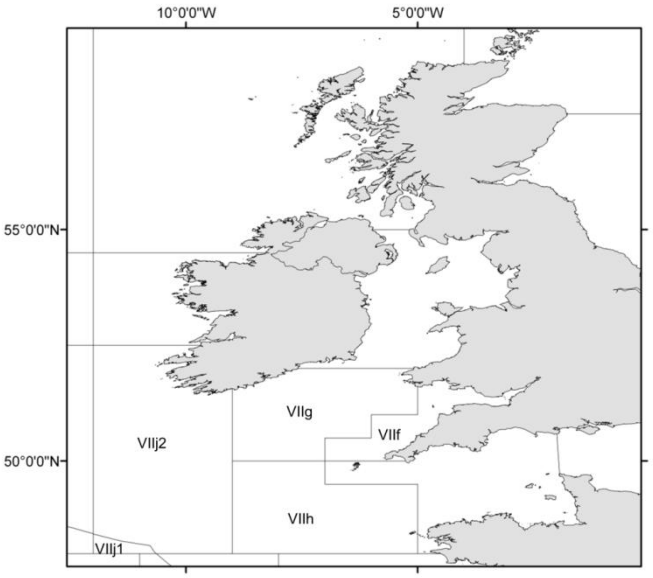

Figure 4.1 Map of the Celtic Sea region identified from the ICES divisions VIIf-g.

The Ecopath with Ecosim model

To construct the trophic interactions occurring in the Celtic Sea ecosystem we used the steady-state simulation program Ecopath with Ecosim. This software is used to recreate a virtual food web and to analyse ecosystem dynamics (Pauly et al., 2000). The concept was originally proposed by Polovina (1984) and has been combined with routines for network analysis and system maturity indices based on the approaches of Ulanowicz (1986) and Odum (1969).

In structuring the model, the species are aggregated and represented as functional groups (FGs) according to their ecology (i.e. habitat, diet composition, life history) and connected via predator/prey interactions based on diet composition. Some of these groups consist of one species or life history stage, whereas others consist of multiple species. For some of these functional groups, species were also aggregated into trophic guilds (e.g. small benthic fish) while other groups were formed on the basis of general taxonomic similarities (e.g. lobsters and crabs) or similar feeding strategy (e.g. seabird offshore-divers). Commercially important fish were divided into juvenile and adult groups and linked in the model using the multi-stanza feature which allows the representation of multiple ontogenic stages (juvenile/adult). Other fish species that are commercially and/or functionally important were represented as single species or grouped at the family level. Similarly seabirds were divided into six functional groups; details are provided in Appendix 3.

For each functional group (*i*), Ecopath requires the input of biomass (B) (t km^{-2}), production/biomass ratio (P/B y-1) which in most conditions correspond to the total mortality rate or instantaneous mortality (Z= fishing + natural mortality, see Allen, 1971), consumption/biomass (Q/B y-1) and ecotrophic efficiency (EE, which expresses the proportion of total production that is used in the system; Christensen and Walters, 2004).

In addition, the model incorporates information on diet composition and fishery statistics (landings and discards). Typically B, P/B, and Q/B are entered for all groups from the literature, stock assessments and ecological studies and EE is estimated from the software.

In the model an equilibrium condition is assumed where group inputs are equivalent to their outputs. To establish this equilibrium condition, a biomass budget equation is determined for each group (*i*) considered as:

Production by (*i*) – predation on (*i*) – non-predation losses of (*i*) – export of (*i*) = 0

Ecopath expresses each term in a budget equation as a linear function of the mean biomass and results in a system of simultaneous equations expressed as:

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i = 0$$

Equation 1

where B*i* is the biomass of the group *i*; P/B*i* is its production rate (assumed equal to the total mortality, Z) as defined in fisheries science (Allen, 1971); EE*i* is the ecotrophic efficiency of *i* (the fraction of the production of *i* that is consumed within the system, exported or harvested); B*j* the biomass of any predator *j* of the prey *i*; Q/B*j* the food consumption rate of *j* and is a parameter that expresses food consumption of an age-structured fish population relative to its biomass assuming that juveniles are more numerous compared to adults and consume much more food (compared to their weight) as documented by Pauly (1986); DC*ji* is the fraction of *i* in the diet of *j*, expressed in percentage of weight; Y*i* is the total catch of *i*; and E*i* is the net migration rate (emigration-immigration) of *i*.

The Ecopath model presented here was developed using Ecopath with Ecosim 5.1 (downloaded from http://www.Ecopath.org). Flows within the model were given in tonnes km^{-2} yr^{-1}. A combination of published and unpublished information specific to the Celtic Sea was used as input parameters (see Appendix 3), but where data were lacking data from other ecosystems was used (Lees and Mackinson, 2007).

Ecopath has an additional dynamic routine called Ecosim, which provides temporal descriptions of the possible trends that might occur in the ecosystem under various fishing strategies or other possible changes in the ecosystem. This time-dynamic simulation model uses mass balance results from the base Ecopath model for parameter estimation.

The Ecosim master equation takes the form:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M_i + F_i + e_i)B_i$$

Equation 2

Where dB_i/dt represents the growth rate during the time interval dt of group i in terms of its biomass B_i; g_i is the net growth efficiency (production/consumption ratio); M_i is the non-predation ('other') natural mortality rate; F_i is fishing mortality rate; e_i is emigration rate; I_i is immigration rate. The consumption rates Q_{ji} are calculated based on the 'foraging arena' concept, where B_i's are divided into vulnerable and invulnerable components (Walters et al. 1997).

Design of the Ecopath model for the Celtic Sea: structure and basic input data

The Celtic Sea model is composed of 64 functional groups including: 3 mammals, 6 groups of seabird, 34 groups of fish, 15 invertebrates, 2 microbial groups, 1 primary producer (phytoplankton) and 3 detritus groups including: particulate organic matter, dissolved organic matter and discarded fish. Descriptions of the functional groups, their

component species, data sources, analyses used in the construction of the model, and a sensitivity analysis are presented in Appendix 3 and summarized in Table A3.4.

Balancing the model

When the required information for each functional group (biomass, P/B, Q/B, diet composition, EE and fishery in the form of landings and discards) was entered into the model, we proceeded with the model parameterization where the missing parameters were estimated, to achieve mass balance.

Before balancing the model a pre-balance diagnostic (PREBAL; Link, 2010) was used to ensure that any potential problems were captured before Ecopath network outputs were used to address research or management questions. PREBAL provides a set of guidelines presented as a form of "checklist" (for details see Link, 2010). Following this we proceeded with the model balancing.

A functional group is considered to be imbalanced where the EE value is larger than 1 (in other words if the total demand placed on a particular group by predation or fishing exceeds the production or mortality of that group). The initial results of the Ecopath parameter estimation routine revealed several groups for which 'demand' was greater than 'supply' (i.e. EE >1). During the balancing process we used the approach proposed by Mackinson and Daskalov (2007) using data "pedigree" (quality and reliability) as a guide to prioritizing and justifying which parameters to change.

Changes were mainly made to P/B estimates which were too low in some cases (P/B values were increased on the basis of other estimates for similar functional groups available in literature), after the diet matrix was scrutinized. Minor diet adjustments were made in cases when predation was too high on a particular functional group; in such instances the contribution of this prey was reduced whilst retaining the original proportions of the other prey in the diet.

Biomass data were examined after the P/B and diet composition, we believe these estimates are reliable and only in a few cases adjustments were made. Since there was a range of biomass calculated in most cases for fish and invertebrates, biomass estimates were changed within these ranges. As fish biomass data were extracted from a bottom trawl survey (originally designed to study demersal fish) the biomass of pelagic species was increased in order to account for model requirement. However these values were comparable to the others of similar ecosystems (i.e. North Sea, Irish Sea). Changes in Q/B were made in some cases, to account for unbalanced groups; these changes were made on the basis of other estimates for similar functional groups available in the literature.

Application of Ecopath routine: Mixed trophic impact

Ecopath has several routines that can be used to better describe the ecosystem and the trophic relationships between species within it. Here we used the Mixed Trophic Impact (MTI) routine (Ulanowicz and Puccia, 1990) to assess the impacts of increased biomass (10%) of a particular group on the biomass of other groups in the system. The MTI routine of Ecopath shows the direct and indirect influences of biomass variations of any functional group on all other groups considered. An initial condition that should be considered for this routine is that diet composition of each functional group does not change in relationship to prey availability. This routine is a tool for indicating the possible impact of direct and indirect interactions (including competition) in a steady-state system and gives useful descriptions of how short-term variations in the food web can affect the whole ecosystem; however it is important to consider that it is not an instrument for making future predictions of what will happen if certain interaction terms are changed. Trophic effects due to changes in the diet composition of functional groups in the ecosystem are addressed in the next chapter with the application of the dynamic model Ecosim.

The MTI is calculated by constructing a n x n matrix, where the i,jth element representing the interaction between the impacting group i and the impacted group j is:

$$MTI_{i,j} = DC_{i,j} - FC_{j,i}$$

Equation 3

Where $DC_{i,j}$ is the diet composition term expressing how much *j* contributes to the diet of *i*, and $FC_{j,i}$ is the term giving the proportion of the predation on *j* that is due to *i* as predator. For the impacted group *j* the direct and indirect impacts due to an increase of the impacting group *i* are calculated. These impacts are calculated by multiplication of the matrix of the direct impact and indirect impact for each of impacted group. The direct impacts describe the effect that an increase of the impacting groups in the system will have on the biomass of the impacted groups, while the indirect impacts can be associated with inter-group competition (i.e. density dependent effects) and trophic cascades.

As fisheries information (landings and discards) for each functional group can be included in Ecopath, when the MTI is computed the potential impacts of an increase in fisheries (modeled as impacting group *i*) are calculated on ecological groups for example fish biomass (impacted group *j*).

Application of Ecopath routine: Niche overlap

The niche overlap (in terms of prey) was calculated in Ecopath using Pianka's (1973) index as modified by Christensen et al. (2005). This routine can be used to calculate the trophic niche partitioning and food competition for each functional group within Ecopath from the proportions of prey in the diet matrix. The index assumes values

between 0 (no overlap), 1 (total overlap), and intermediate values show partial overlap in resource utilization.

4.3 RESULTS

The Ecopath model

The output parameters of the balanced model are shown in Table 4.1, whilst the trophic relationships are summarized in Fig. 4.2. For each functional group the trophic level (TL) was calculated in Ecopath based upon diet composition. However, the trophic level of two seabird groups (offshore-surface feeders, and gulls) were slightly underestimated by Ecopath (respectively 3.82 and 2.46) due to the contribution of discards in their diet composition which were given a low trophic level (TL=1) in the model.

The total fisheries catch amounted to 6.040 tkm^{-2} yr^{-1} at a mean TL of 3.80, with the highest catches being planktivorous fish (pelagic fish, mackerel and horse mackerel), piscivorous fish (cod, whiting and monkfish) and macrocarnivorous fish (rays and skates). The total amount of detritus in the ecosystem is estimated in Ecopath as 5932.01 tkm^{-2} yr^{-1}.

Mixed trophic impact

The results of the MTI routine for seabird functional groups are shown in Fig. 4.3, where the main impacting groups affecting seabirds are also shown. These were selected on the basis of their importance in the seabird diet composition or in the food web. Our results showed that seabird inshore divers and offshore divers are negatively affected by gulls, while an increase in pelagic fish biomass is beneficial for most of the seabird groups (offshore-surface feeders, inshore divers, off-shore divers and Manx shearwater; Fig. 4.3). In addition, an increase in small benthic fish has a positive impact on seabird inshore divers; while European storm petrel benefits from an increase in Trisopterus spp. and small crustaceans. Manx shearwater is positively affected by an

increase in squid biomass. Discard production has a positive effect on scavenger seabird groups such as offshore-surface feeders and gulls (Fig. 4.3).

Niche overlap

The results of the niche overlap routine for seabird functional groups are shown in Fig. 4.4, only groups with the highest niche overlap are presented. Seabird offshore-surface feeders had very similar foraging behavior to other apex predators such as gulls (value = 0.54). However, some overlap in resources utilization occurred with both small sharks (value = 0.49), and fish top-predators (Fig. 4.4).

The niches of seabird inshore divers overlapped with those of apex predators, notably with those of seabird offshore divers (value = 0.65), baleen whales (value = 0.64), large sharks (value = 0.58) and Manx shearwater (value = 0.51); therefore some overlap, in terms of prey items, was found with some pelagic fish consumers (garfish; value = 0.64).

Similarly, the niche occupied by seabird offshore divers also overlapped completely with baleen whales (value = 1) and other apex predators in the ecosystem (i.e. large sharks 0.66; Manx shearwater 0.65; and seabird inshore divers 0.65), however some overlap in resources utilization occurred with other pelagic fish consumers (garfish; value = 0.77) (Fig. 4.4).

The niche of gulls overlapped with seabird offshore-surface feeders (value = 0.54). In some cases some minor similarity occurred in terms of prey items with other fish top predators such as rays and skates (value = 0.26), gurnards (value = 0.24), and seabass (value = 0.77).

Similarly, Manx shearwater showed an overlapped niche with seabird offshore divers (value = 0.65), baleen whales (value = 0.65) and seabird inshore divers (value = 0.51),

however an overlap in terms of prey was found with pollack and saithe (value = 0.75). European storm-petrel overlapped little with other seabirds and other apex predators, but showed some minor similarity in terms of prey with fish groups such as megrim (value = 0.34), whiting and haddock (value = 0.26) as is shown in Fig. 4.4.

Table 4.1 Parameterization of the Ecopath model for the Celtic Sea. B: Biomass; P/B: Production/Biomass ratio (instantaneous rate of total mortality); Q/B: Consumption/Biomass ratio (consumption represents the intake of food by a group); EE: Ecotrophic Efficiency express as fraction of the production of i that is consumed within the system, exported or harvested.

	Group	Trophic level	B (t/km2)	P/B (per year)	Q/B (per year)	EE
1	Baleen whales	4.59	0.063	0.020	6.323	0
2	Toothed whales	4.73	0.0397	0.060	18.595	0.315
3	Seals	4.71	0.0048	0.085	15.857	0.324
4	Seabird offshore-surface feeders	3.82	0.00102	0.374	98.778	0
5	Seabird inshore-divers	4.48	0.000107	0.130	106.101	0.463
6	Seabird offshore-divers	4.59	0.000702	0.450	94.176	0.815
7	Gulls	2.46	0.000564	0.210	56.000	0.451
8	Manx shearwater	4.42	0.000734	0.141	205.612	0
9	European storm petrel	3.67	0.00000119	0.270	270.000	0
10	Cod	4.54	0.450	0.900	3.400	0.938
11	Juvenile cod	3.8	0.109	1.200	8.512	0.617
12	Blue whiting	3.54	0.444	1.000	6.666	0.97
13	Juvenile blue whiting	3.36	1.819	2.200	19.26	0.715
14	Hake	4.55	0.260	0.774	3.529	0.888
15	Juvenile hake	4.43	0.401	0.895	7.024	0.826
16	Plaice	3.08	0.040	0.892	5.131	0.436
17	Juvenile plaice	3.54	0.075	1.900	14.695	0.685
18	Megrim	4.46	0.194	0.994	3.100	0.779
19	Juvenile megrim	3.87	0.057	1.300	7.777	0.948
20	Whiting	4.5	0.412	1.720	3.874	0.996
21	Juvenile whiting	4.14	0.623	3.400	10.131	0.524
22	Monkfish	4.58	0.290	0.851	1.900	0.887
23	Juvenile monkfish	4.34	1.105	1.084	4.619	0.759
24	Haddock	4.4	0.169	0.773	4.657	0.713
25	Juvenile haddock	3.14	0.035	1.100	11.317	0.695
26	Sole	3.1	0.058	1.000	5.722	0.976
27	Mackerel	3.51	14.652	0.651	1.730	0.95
28	Horse mackerel	3.46	7.366	0.707	3.510	0.95
29	Red mullet	3.16	0.070	0.733	5.962	0.661
30	Sea bass	4.08	0.408	0.779	4.407	0.362
31	Large sharks	4.68	0.646	0.819	3.000	0.002
32	Small sharks	4.01	1.521	0.113	4.739	0.205
33	Pelagic fish	3.59	4.480	2.900	7.916	0.983
34	Rays and Skates	3.75	0.879	0.387	3.798	0.788
35	Turbot and Brill	3.37	0.305	0.592	5.324	0.071
36	Small and medium flatfish	3.4	1.450	2.900	5.800	0.956
37	Trisopterus spp.	3.44	2.000	2.500	7.461	0.752
38	Gurnards	3.4	0.406	0.689	5.621	0.676
39	Pollack and Saithe	4.18	3.818	0.787	3.582	0.151

Table 4.1 (continued) Parameterization of the Ecopath model for the Celtic Sea. B: Biomass; P/B: Production/Biomass ratio (instantaneous rate of total mortality); Q/B: Consumption/Biomass ratio (consumption represents the intake of food by a group); EE: Ecotrophic Efficiency express as fraction of the production of i that is consumed within the system, exported or harvested.

	Group	Trophic level	B (t/km2)	P/B (per year)	Q/B (per year)	EE
40	Small benthic fish	3.08	0.900	3.28	8.682	0.888
41	Small pelagic spp.	3.57	2.550	1.200	9.246	0.846
42	Garfish	3.81	0.041	0.676	4.870	0.95
43	Demersal predators	4.46	0.570	0.779	3.938	0.821
44	Small crabs and other decapods	2.25	9.100	3.100	6.332	0.942
45	Large crabs and lobsters	2.43	0.393	2.300	4.400	0.742
46	Small crustaceans	2	0.960	3.456	23.040	0.815
47	Bivalves	2	25.320	1.104	12.266	0.63
48	Gastropods	2	1.765	0.655	4.367	0.718
49	Cuttlefish	4.2	0.220	4.500	15.000	0.874
50	Squid	3.37	2.194	3.000	15.000	0.95
51	Sessile invertebrate	2.78	3.811	0.645	2.580	0.784
52	Echinoderms	2.25	7.459	1.376	5.504	0.298
53	Polychaetes	2	20.815	1.963	13.088	0.365
54	Nematoda	2.1	0.070	3.300	16.667	0.855
55	Zooplankton	2.56	19.772	9.700	60.000	0.955
56	Carnivorous macroplankton	3.56	0.700	9.500	23.330	0.989
57	Euphausiids	2.37	20.150	6.600	22.000	0.875
58	Microflagellate	2.7	2.100	200.000	400.000	0.932
59	Pelagic bacteria	2	3.000	210.000	420.000	0.933
60	Benthic bacteria	2	3.247	110.000	220.000	0.23
61	Phytoplankton	1	40.477	120.000	-	0.232
62	Particulate organic matter	1	56.850	-	-	0.237
63	Discards	1	1.395	-	-	0.034
64	Dissolved organic matter	1	268.837	-	-	0.749

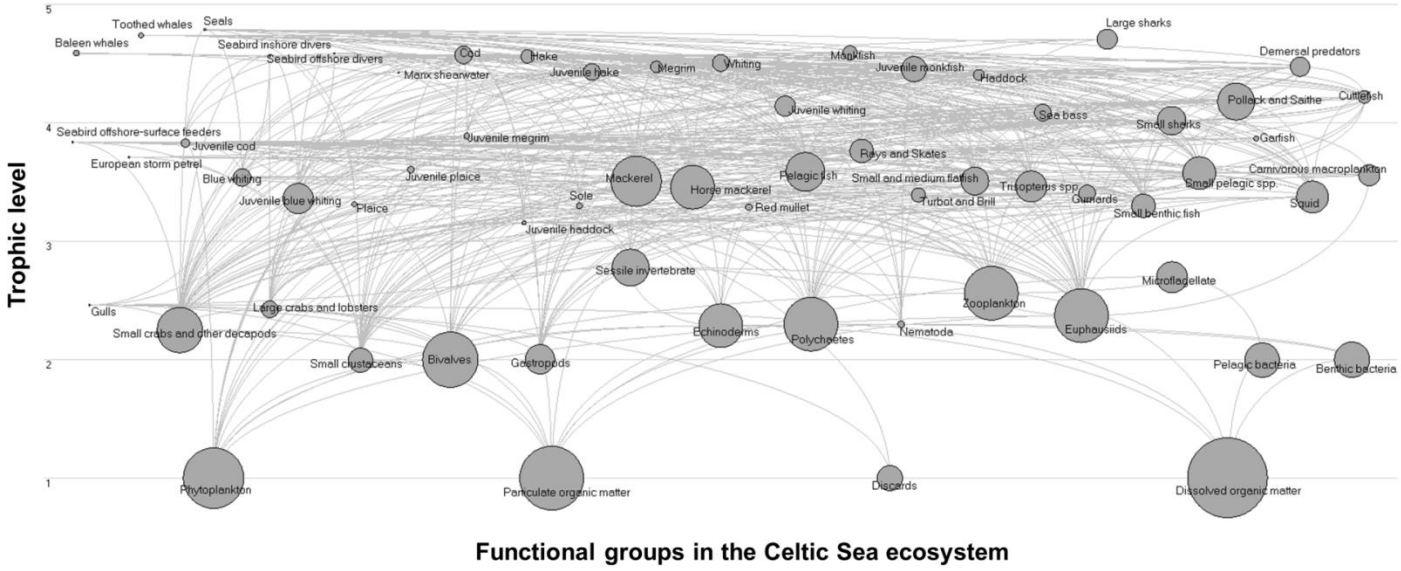

Figure 4.2 The Celtic Sea Ecopath model in terms of relative biomass (size of circles) and its major energy flows within Functional Groups (FGs). The horizontal axis of symmetry of each box is aligned with the trophic level of this box. The value of a trophic level is a fractional because it depends on the diet composition of this group and on the trophic levels of its preys (Christensen and Pauly, 1993). Note that TL for Seabird surface feeders and Gulls the values were under estimated by Ecopath (respectively 3.82 and 2.46).

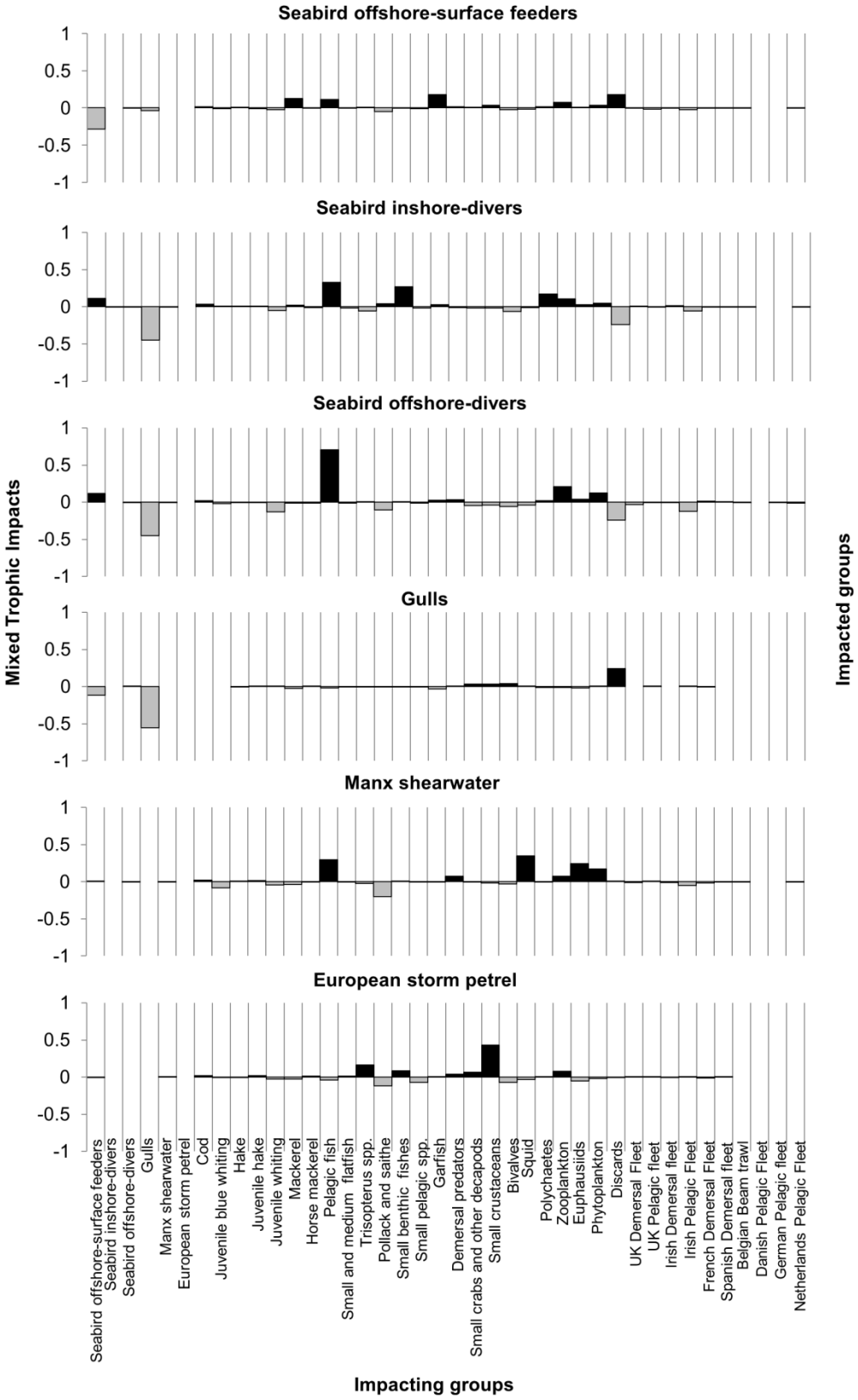

Figure 4.3 The Mixed Trophic Impacts Analysis in the Celtic Sea ecosystem. Seabird (impacted groups) response to the increase (by 10%) of other groups (impacting groups) biomass in the system. Positive impacts are shown above the base line in black (above the line) and negative impacts below in grey (below the line).

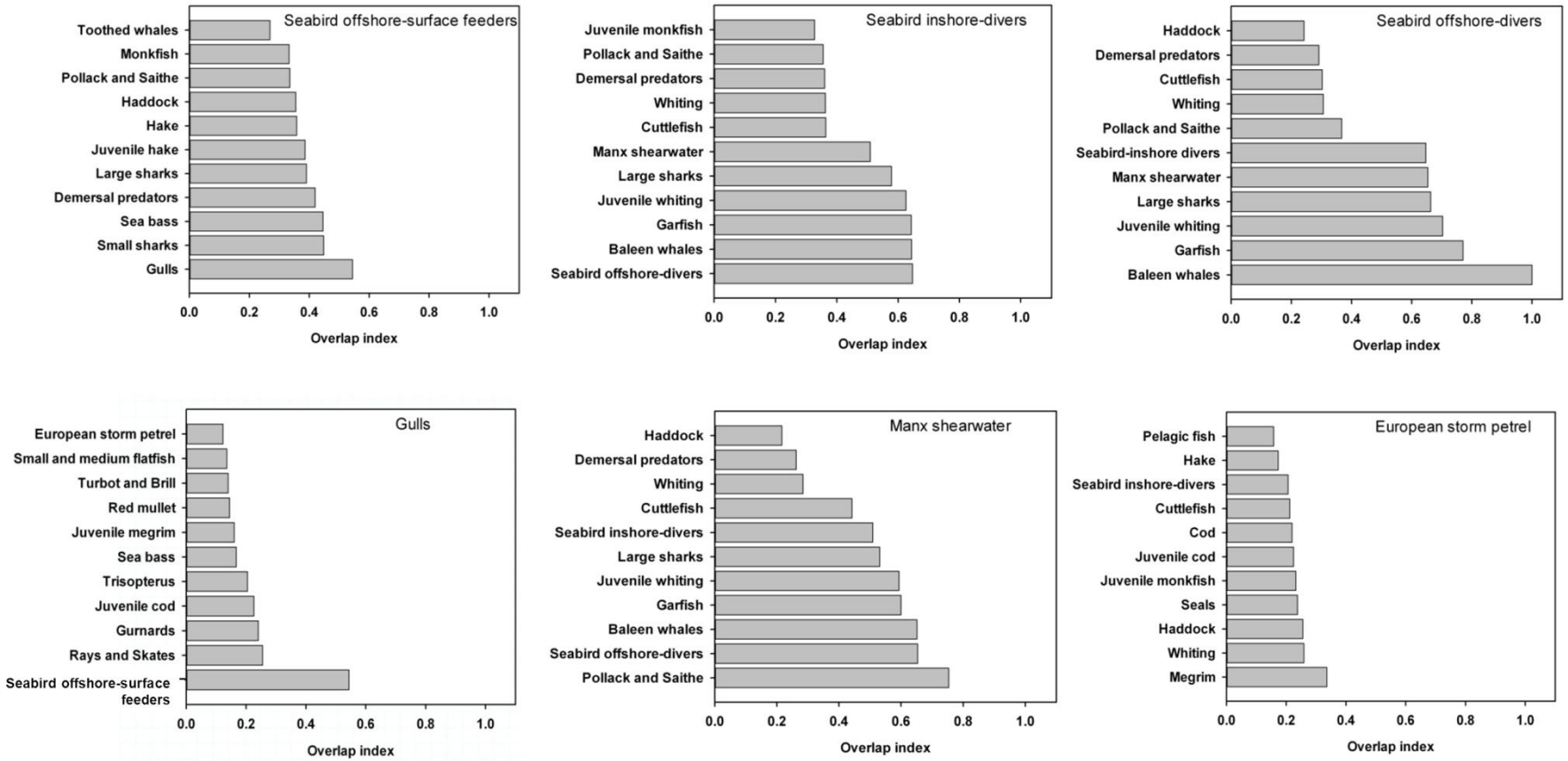

Figure 4.4 Trophic niche overlap index for seabird groups in the Celtic Sea calculated from the proportions of used resources in the diet matrix. Only groups with the highest values are shown. The index assumes values between 0 (no overlap) and 1 (total overlap).

4.4 DISCUSSION

Several modeling approaches have been used to manage marine ecosystems from single or multiple-species models to the application of a more complex ecosystem-based approach (Garcia et al., 2003). Within these modeling approaches (reviewed by Plagayni, 2007), Ecopath with Ecosim models are currently the most comprehensive tools which allow the description of the structure of a marine ecosystem and quantify the effects of human activities on the trophic food web.

The EwE model has been widely used by more than 2400 registered users in 120 countries around the world (Christensen and Walters, 2004). Around the UK waters this approach has been applied to other ecosystems such as the Irish Sea, English Channel and West Scotland (Lees and Mackinson, 2007; Stanford and Pitcher, 2004; Heymans et al., 2011). The Celtic Sea Ecopath model presented in this study is one of the most complex (64 functional groups) developed, although it has fewer functional groups than a North Sea model (68 functional groups; Mackinson and Daskalov, 2007). The importance of the degree of complexity of an ecosystem-based model structure (complex versus simpler models) has been discussed in the past, suggesting that both simple and complex models seem to have different system consequences to applied disturbance (Pinnegar et al., 2005). However, there is not a better way to proceed, but each model needs to be configured to address a specific ecological question. The Ecopath model for the Celtic Sea ecosystem describes the trophic interrelations among functional biological groups with particular reference to the role of seabird apex predators.

Trophic structure and functioning of the ecosystem

Odum (1969) formulated a theory to predict the long-term response of ecosystems over evolutionary time (or under stress) that incorporates elements of trophic links, of size, of

(bottom) structure, and of communities of species. He described how systems tend to develop toward maturity over time, how ecosystems change when stress is applied to them, and discussed how this would be reflected through a series of attributes discussed in Christensen and Pauly (1998). The analysis of the trophic structure of the Celtic Sea shows that it is a mature ecosystem in terms of biomass supported/energy flow, total organic matter, the role of detritus (Fig. 4.2), as well as narrow niche specialization (Fig. 4.4). The analysis of the ecosystem trophic structure showed that higher trophic level values (TL) are recorded for apex predators such as toothed whales, seals, large sharks and seabird groups with the exception of gulls and offshore-surface feeders where the trophic level was underestimated in Ecopath. This is due to the fact that part of their diet is attributed to discards, which in the model are calculated to have TL=1, as they are considered "dead" and therefore given the same trophic level as detritus. For the remaining groups the model estimations of trophic levels were considered reasonable and comparable to other Ecopath models (Lee and Mackinson, 2007; Mackinson and Daskalov, 2007 (Table 4.1).

Seabird groups are impacted by changes in biomass at the base of the food web (such as phytoplankton, zooplankton) and mid-trophic level groups such as pelagic fish (clupeids, garfish and mackerel) (Fig. 4.3). These typical trophic effects have been described in other marine ecosystems in the North Atlantic (i.e. North Sea, Bering Sea) for seabird offshore surface feeders and offshore divers (Aebischer et al., 1990; Hunt et al., 2002). A similar but less marked response was shown for seabird inshore divers, probably due to the fact that they also forage on other groups such as small benthic fish (Liliendandahl and Solmundsson, 2007; Birkead et al., 2007).

Our model reveals that increases in pelagic fish biomass have a positive effect on seabird functional groups in the Celtic Sea. Small schooling pelagic fish (such as pilchard *Sardina pilchardus* (W.), herring *Clupea harengus* and sprat *Sprattus sprattus*))

play an important role in many other marine systems by transferring energy across multiple trophic levels (Cury et al., 2000) and in some cases these species can have both top-down and bottom-up effects (i.e. wasp-waist control; Rice, 1995). Recent studies have shown how chronic food scarcity as a result of fishery impacts could compromise some seabird populations with dramatic ecological effects worldwide highlighting the need of ecosystem based studies (Cury et al., 2011).

Gulls were not particularly sensitive to changes in the biomass of pelagic fish, but were instead heavily influenced by changes in discard production, as were offshore-surface feeders that also rely heavily on discards. This indirect effect of fisheries, seems to play a substantial role in the regulation of seabird communities (Votier et al., 2004). Our results suggest that in the Celtic Sea food web, scavenger seabird groups (such as offshore-surface feeders and gulls) seem to benefit from an increase in discards in the system, this effect has been previously described for northern gannet *Morus bassanus* (Votier et al., 2010). The increase of some seabird species (i.e. gulls) in the ecosystem could have, in turn, a negative effect on seabirds inshore and offshore divers.

Seabird trophic relationships

Seabirds in the Celtic Sea exhibit a degree of niche overlap with other apex predators (sharks, marine mammals) in the ecosystem, except where the main competitors are fish top predators (Fig. 4.4). Our results show that seabird offshore-surface feeders overlap closely with gulls, partly because of discard consumption (Votier et al., 2010). In addition, a partial overlap is also shown with small sharks; however, while there might be overlap in terms of prey items (i.e. mackerel and pelagic fish), the likelihood of direct competition is unlikely because of the lack of spatial overlap.

Moreover, extensive niche overlap occurs among several seabird groups (seabird inshore and offshore divers), baleen whales and garfish (Fig. 4.4), and is due to the competition for pelagic fish. These trophic interactions and competition for pelagic fish

amongst apex predators (marine mammals, seabirds, and fish top predators) have been described in other marine systems (Overholtz and Link, 2007), suggesting that apex predators are especially vulnerable when marine resources become overexploited (Camphuysen, 2001), particularly small pelagic fish (Furness, 2002).

The European storm-petrel does not seem to be competing for resources with other seabird groups (Fig. 4.4). Despite this, some niche overlap was found with other fish top-predators (i.e. megrim) due to the fact that both feed upon Trisopterus spp.; however we assumed that these two species are very unlikely to be in competition for the same resources because of their marked spatial separation. Similar trophic mechanisms have been described for fish and invertebrate species elsewhere (Attrill and Power, 2004).

Model assumptions and limitations

The EwE modeling approach is useful in describing marine ecosystem food webs and dynamics, and its capabilities have been constantly improved since it was first developed (Christensen and Walters, 2000), but caveats and limitations (discussed in Christensen and Walters, 2000) need to be considered in the formulation of management plans for marine resource conservation. In undertaking an integrated and quantitative analysis of the whole ecosystem, the model must represent relatively broad components and processes. Because species in the model are aggregated into functional groups this can be a source of uncertainty due to the over or under estimation of fishing mortality, or cannibalism, for example. Scarcity of data and such uncertainty in the information about ecosystems (i.e. biomass data) influences the usefulness of ecosystem models; however, an appropriate application of the model, with recognition of its limitations, can facilitate the interpretation of the results obtained.

4.5 CONCLUSIONS

Trophic interactions in the Celtic Sea ecosystem were described by using an Ecopath model. The application of such a complex model represents an important attempt to integrate the available biological data for the Celtic Sea into a coherent format, in order to give a comprehensive ecosystem description that can be used to support future studies. Seabirds have an important role in maintaining community assemblage in the Celtic Sea. They prey on a wide range of trophic groups and thus provide numerous linkages between species in the ecosystem. Such linkages are important in controlling food web structure, and they favor ecosystem stability (Parsons, 1992). The results presented here indicate that other groups are also important in the functioning of the ecosystem. Of particular importance are pelagic fish that play a key role in the Celtic Sea food web by transferring energy from the base up to the apex predators. In addition, seabirds are also vulnerable to fisheries indirect effects (discard production), and this aspect needs to be taken into consideration for future management plans.

The application of Ecopath combined with Ecosim models can be useful in addressing ecological questions regarding processes or long-term impacts (such as climate variation and fishing activity) that can occur in the whole Celtic Sea ecosystem, and in some cases can be used as a guide to explore possible impacts and the implications of alternative broad policies in order to facilitate policy-making decisions. The application of Ecopath alone only gives an instantaneous snapshot of the biomass and energy flows in the functioning of the ecosystem, and cannot be used to assess the effect of policy changes (such as changes in fishing rates). This limitation is overcome by combining Ecopath with the dynamic module Ecosim. The advantages of using Ecosim and its application for the Celtic Sea ecosystem are discussed further in Chapter 5.

Chapter 5

Predicting fishing and climate effects on marine apex predators in the Celtic Sea using a tropho-dynamic simulation model

Abstract

It is clear that fisheries and climate change affect marine ecosystems, although the combined impact of these stressors is less clearly understood. Under future climate change predictions and fisheries reform (i.e. the EC Common Fishery Policy or CFP), the Northeast Atlantic is likely to be severely affected. Understanding how marine ecosystems will respond to these changes requires the use of predictive ecosystem modeling.

The aim of this study was to investigate the combined effects of changes in fisheries management and climatic conditions in the Celtic Sea ecosystem, a productive area in the Northeast Atlantic, focusing particularly on the response of seabirds. Using a tropho-dynamic model Ecosim (which belongs to Ecopath with Ecosim) we examine and predict the influence of different fishery regimes and changes in primary production driven by climate change scenarios upon seabirds. We tested for different fisheries and climate scenarios: 1) diverse fishing strategies (Maximum Sustainable Yield, Status quo or no change, High fishing effort) on pelagic fish species and consequent effect on seabirds; 2) application of a discards ban and relative effects on scavenger seabirds. 3) sea temperature rising while keeping constant fishing effort; and 4) sea temperature rising with changes in fishing effort.

Our results showed the relative impacts that the application of different fisheries regimes under the CFP (i.e. application of quota, discards ban) and climate change may have upon seabirds and their diverse response. In particular the application of fishing regimes associated with the MSY on pelagic fish showed a positive effect on seabirds, especially offshore divers. Therefore, the simulation of the discards ban on the Celtic Sea ecosystem predicted a decline in scavenger seabird biomass (gulls and offshore-surface feeders). Moreover, results from the combination of both fishing and climate impacts provided evidence that the effect of climate forcing can outweigh that of fishery for some seabird species, highlighting that both of these factors need to be considered in resource management plans and biodiversity conservation of the Celtic Sea ecosystem.

5.1 INTRODUCTION

Commercial fishing and climate variability are affecting the biodiversity, structure and functioning of marine ecosystems (Stockstad, 2006; Guldenberg and Bruno, 2010). Although several studies have tried to explain the effect of these impacts on marine food webs (Jennings and Kaiser, 1998; Beaugrand et al., 2008), it is unclear to what extent fishing and climate change may influence marine ecosystems (Kirby et al., 2009). A key goal of marine scientists is, therefore, to understand current and future impacts of both fisheries and climate change to better inform marine management practices.

Commercial capture fisheries represent one of the most pervasive impacts upon marine ecosystems and this pressure has increased over time (Pauly et al., 2005), with global impacts on sustainability (Pauly et al., 2002), and transformation of the community structure and function of marine food webs (Pauly et al., 1998). As well as reducing stocks of most commercial species, fisheries have wider direct and indirect ecosystem level impacts. Fisheries directly affect marine ecosystems by removing larger piscivorous species, leading to an increase of smaller pelagic species via predator

release, reflected in the reduction of mean trophic level and size of landings (Pauly et al., 1998; Blanchard et al., 2005). In addition, fisheries directly compete with marine predators for food (Furness and Camphuysen, 1997) and the production of huge quantities of unwanted catch and offal that is discarded at sea may have profound implications for ecosystem health (Kelleher, 2005).

In addition to fisheries impacts, global climate change is affecting marine ecosystems by altering oceanographic conditions (e.g. sea temperature and ocean circulation patterns). These changes have affected the distribution and biology of marine species, leading to a loss of habitat and biodiversity (Guldberg and Bruno 2010). Climate change may impact upon marine food webs in different ways: for example, by influencing species physiology (e.g. metabolism), or controlling the prey availability for top-predators (bottom-up control; Ottersen et al., 2001, 2004b). In the north-eastern part of the North Atlantic Ocean, recent large-scale biogeographical changes in the biodiversity of a key zooplankton group (calanoid copepods) has been attributed to increasing sea surface temperature (Beaugrand et al., 2009). These changes have also been propagated through the food chain to affect fish species (Beaugrand et al., 2008) and ultimately apex predators (Luckzac et al., 2011).

Marine ecosystem responses to such pressures can be difficult to disentangle and the utilization of opportune indicators is necessary. Apex predators, such as seabirds, are key consumers in marine ecosystems and can act as sentinels for short and long-term changes in fish stock size or oceanographic conditions (Hunt and Schneider, 1987; Croxall et al., 1988; Kitaysky and Golubova, 2000). Fisheries may impact seabirds via accidental bycatch (Anderson et al., 2011), or industrial fisheries may compete with seabirds for the same resource (e.g. Frederiksen et al., 2004a). Alternatively discards may provide an important subsidy for seabirds (Kelleher, 2005), although changes in

discarding may have unforeseen knock-on consequences if scavenging populations become large (Votier et al., 2004, 2010).

In addition to fisheries impacts, changing climatic conditions have had particularly severe effects upon seabird populations, impacting them directly via changes in temperature (Oswald et al., 2008) or storm frequency (Frederiksen et al., 2008b). Indirect effects are mediated via changes in food availability, having negative impacts on reproductive success, survival (Frederiksen et al., 2004b) and recruitment (Crespin et al., 2006). Such changes may threaten the long-term viability of some seabird populations (Wanless et al., 2005, Frederiksen et al., 2006). Moreover, it is unclear how on-going warming trends will impact seabird populations in the future, particularly when interacting with fishery pressure.

A comprehensive approach to marine ecosystem management requires assessment of the range of fisheries related impacts, in tandem with climate related change. In recent years, improvements have been made with movement away from single-species towards holistic Ecosystem-based Approaches for Fishery management (EAF; Link, 2002; FAO, 2003). This is a key goal toward sustainable fisheries (Garcia et al., 2003; Pikitch et al., 2004), and was highlighted in the most recent EU Common Fishery Policy (CFP) in 2008 (currently in reform since 2009). The purpose of the reform is to restore overexploited European fish stocks by the application of several management measures by 2015 including the application of the Maximum Sustainable Yield (MSY: maximum annual catch which can be taken from a fish stock without reducing its productivity) and a discards reduction/ban. Most of the European fish stocks have been fished down, with the 88% of Community stocks being fished beyond the MSY (and 30% of these stocks being outside safe biological limits) (EU, 2008). Although the details have yet to be formalised, reform of the CFP represents the most fundamental change to the way in which European fisheries are managed for many decades. Scientists have discussed the

effects, at ecosystem level, of applying MSY, or discard reduction (Pikitch et al., 2004; Froese et al., 2008; Hilborn, 2011; Bellido et al., 2011); however no studies have yet shown what the impact might be upon apex predators such as seabirds. In summary, changes in climate and fisheries management are likely to have a range of complex impacts upon seabird populations, but how these interact and how they may change in the future remains an important unanswered question.

The goal of the present study is to investigate the combined effects of fisheries reform in the CFP together with predicted climatic change (using scenarios from the latest Intergovernmental Panel on Climate Change; IPCC, 2007) on seabirds in the Celtic Sea. We use a tropho-dynamic simulation model Ecosim (which is a module of the software Ecopath with Ecosim) to evaluate the effects of changing primary production and fisheries regimes on the food web, and link these with changes in seabird biomass. First we model three different pelagic fisheries management scenarios: (1) MSY, (2) status quo, (3) increased fishing effort. Second we model a ban on discarding. Third we model a rise in sea temperature consistent with IPCC predictions, but maintain constant fishing effort. Finally we model the impact of rising sea temperature at the same time as reduced fishing effort.

5.2 MATERIALS AND METHODS

The study area

The Celtic Sea is situated to the southwest of Great Britain, corresponding to ICES divisions VIIf-j. This region represents a transition zone between the Atlantic Ocean and the coastal waters of the Bristol Channel and Irish Sea (OSPAR, 2002). This region is particularly important due to its high biodiversity in terms of apex predators (i.e. seabirds, marine mammals; Mitchell et al., 2004; Hammond et al., 2006), fish and

invertebrate species (Ellis et al., 2002), but also supports fisheries of several European countries (i.e. France, Ireland, UK, Spain and Belgium) (Pinnegar et al., 2002).

Overview of the Ecosim approach

The Ecopath with Ecosim approach has been used worldwide to describe marine ecosystems (Christensen and Walters, 2004). In Chapter 4 and Appendix 3 details of the Celtic Sea Ecopath model are described. The output of the Ecopath model (which provides a snapshot of the ecosystem in terms of energy or mass flow) is the starting point for temporal simulations carried out in Ecosim. This dynamic module provides biomass predictions for each group in the ecosystem in response to direct changes in fishing pressure, predation, or food availability and to indirect changes in fishing or predation on other groups with which a specific group interacts (Christensen et al., 2000).

A key concept of the Ecosim approach is the foraging arena theory, where the prey biomass availability is allocated into "vulnerable" and "safe" stages (Walters and Martell, 2004); the parameter that controls the rate of exchange of prey biomass between the two states is called vulnerability (vulnerable and invulnerable to predation; Walters et al., 1997). It determines the strength of interactions between predators and prey in terms of the increase in mortality rate that a predator can exert on a prey group. Low values of vulnerability (close to 1) mean that an increase in predator biomass will not cause any noticeable increase in mortality due to predation on a given prey (so the system is more likely to be under bottom-up control), while higher values of this parameter mean that predator consumption can control prey biomass (top-down control). This parameter can be estimated in Ecosim using a nonlinear procedure that fits predicted Ecosim biomass time-series to observed biomass time-series (Walters and Martell, 2004; Mackinson et al., 2009). Model stability and sensitivity tests for different

vulnerability setting were performed prior to fitting the model with observation data. Detailed information on model sensitivity and fitting is provided in the Appendix 4.

Data used for the Ecosim model

In Ecosim, observation data are used to drive the model and provide a history of changes in the biomass, against which the model predictions are compared. Time series data from 1991 to 2005 for 4 seabird groups, 10 fish groups, 3 planktonic groups, and environmental variables were collated. Relative biomass of seabird, fish and plankton groups were used to drive the model whilst environmental data were included to force primary producers biomass (Appendix 4, Table A4.1).

Seabird data

We obtained seabird abundance data from the Seabird Monitoring Programme Database at www.defra.jncc.gov.uk/smp. Relative biomass was calculated by multiplying the number of each species by their respective mean body mass (body mass was calculated assuming an equal sex ratio) (Snow and Perrins, 1998). These values were summed to obtain a final seabird biomass estimate for the region. Functional groups (FGs) and the model structure have already been described in Chapter 4 and its Appendix 3.

Fish and plankton data

For fish functional groups, both fishing mortality and relative biomass data were derived from ICES assessment working groups available at http://www.ices.dk/indexfla.asp, while temporal trends of biomass for phytoplankton and zooplankton functional groups (zooplankton and euphausiids) were obtained from the Continuous Plankton Recorder data held at the Sir Alister Hardy Foundation for Ocean Science (SAHFOS).

Environmental variables

In fitting the Celtic Sea model environmental variables were used to drive changes in Primary Production (PP); an explorative data analysis was conducted to identify those environmental time series data best accounting for observed changes in the lower trophic levels of the Celtic Sea food web. Different climate predictors were tested as the forcing function on Primary Production (PP) in the model (see Appendix 4). Winter SST was selected as the best overall model fit determined by the minimum difference between model predictions and time series observations (weighted sum of squares (SS) differences between log reference and log predicted biomass; Christensen et al., 2005). Sea Surface Temperature data were derived from satellite images and collated from the POET database available at http://poet.jpl.nasa.gov with a spatial resolution of 0.04º longitude x 0.04º latitude. Prior to fitting the model

Ecosim simulations

To assess the impact of fishery management strategies and climate variability on apex predators (seabirds), four simulation scenarios were created: two fisheries scenarios (varying fishing mortality of pelagic fish and a ban on discarding), one climate forcing scenario (with fishing pressure held constant) and another combining fishery and climate effects. Based on the output of model fitting we tested these scenarios on three seabird functional groups (Table 5.1). Details of these scenarios are presented below.

Table 5.1 Seabird and pelagic fish functional groups (FGs) used in the Ecosim scenarios. Seabird functional groups are adapted from JNCC, 2008. FGs structure in the model has previously described in Chapter 4 and Appendix 3.

Functional group	Species
Seabird offshore-surface feeders	Northern gannet (*Morus bassanus*) Black-legged kittiwake (*Rissa tridactyla*) Northern fulmar (*Fulmarus glacialis*)
Seabird offshore divers	Common guillemot (*Uria aalge*) Atlantic puffin (*Fratercula artica*) Razorbill (*Alca torda*)
Gulls	Lesser black backed gull (*Larus fuscus*) Herring gull (*Larus argentatus*) Black headed gull (*Larus ridibundus*)
Pelagic fish	Pilchard (*Sardina pilchardus*) Herring (*Clupea harengus*) Sprat (*Sprattus sprattus*) Anchovy (*Engraulis encrasicolus*)

1. Scenario: changes in fishery mortality of pelagic fish

Fisheries compete directly with seabirds, particularly small schooling pelagic fish such as sprat (*Sprattus sprattus*), herring (*Clupea harengus*), and lesser-sandeel (*Ammodytes marinus*), which form a significant part of the diet of many seabirds (Furness, 2002). To test for possible direct fisheries effects on seabird groups we ran three simulations, each spanning 30 years. For each scenario we extracted seabird biomass estimates from the model at 5-year intervals (with much of the biomass change occurring within 5 years of the change in fishing pressure). Vulnerabilities were set as shown in the Appendix 4 (Table A4.4). In these simulations the fishing mortality (F) for pelagic fish was altered as follows:

a) MSY scenario: F was set to 0.25 from 2015 and held constant until 2035. This is the value of MSY proposed by ICES for herring (Froese et al., 2009; Fig. 5.1a) (meaningful values for other similar pelagic species are not available as they are not currently under stock assessment). The aim of this scenario was to test for possible long-term effects on seabirds after the application of the maximum allowable sustainable quota.

b) "Status quo" or *No-change scenario:* this scenario aims to predict future impacts on pelagic fish and seabirds (Fig 5.1b) if there is no change in the current fisheries policy. Fishing mortality values were adjusted according to the trend over the period 2006-2009 and modified onwards from 2015.

c) High fishing impact followed by a no-take scenario: This scenario simulated the potential "opening of new fisheries" in the Celtic Sea, which principally target small pelagic fish (Pinnegar et al., 2002). In particular, based on ICES stock assessment data (http://www.ices.dk/datacentre/StdGraphDB.asp), the long-term value of F for herring was doubled for 10 years from 2015 (2015-2025), followed by a no-take ban for a further 10 years (2025-2035) (Fig. 5.1c).

2. Scenario: discard ban

A key part of the CFP reform is a reduction or cessation of the practice of discarding. Changes in discard availability were applied in the model to test for indirect effects of fisheries on scavenger seabird groups: offshore surface feeders and gulls. In this scenario we stopped discard production, but kept fishing effort constant. We extracted seabird biomass estimates from the model for 2020 (5 years after the proposed start of the discard ban which will take place in 2015 www.defra.gov.uk/environment/marine/cfp/). In order to account for possible adjustments in seabird foraging behavior in response to changes in environmental conditions, we modeled the same scenario, but increased the time that seabirds spend

foraging (Pinaud et al., 2005). Vulnerabilities were set as shown in the Appendix 4 (Table A4.4).

3. Scenario: increasing sea temperature

To test for possible indirect climate effects on seabirds, a simulation was conducted where the PP in the model was forced by increasing WSST by 2 ºC, while fishing effort was held constant. The biomass of each seabird group (offshore-surface feeders, offshore-divers and gulls) were recorded at 5-year intervals for a period of 20 years. Vulnerabilities were set as shown in Appendix 4 (Table A4.4) with the only modification being the interaction between gulls and offshore divers, where the v value was set at 1.4; this is because the interaction between these two groups (gull predation on offshore divers) was sensitive to changes in v, and under this scenario we primarily wanted to test for climate forcing, but retaining inter-species relationship among seabird functional groups.

4. Scenario: combining fisheries and climate effects

To assess the combined effects of fishing and climate variation on seabirds, changes in fisheries regimes were included in the previous scenario (scenario 3: increasing sea temperature). In particular fisheries effort was held constant from 2010-2015 and then reduced by 50% from 2015 onwards. This projection aims to show the potential for combined impacts of climate change and fisheries reform on seabirds. We extracted seabird biomass estimated from the model at 5-year intervals over a period of 20 years and vulnerabilities were set as in the previous scenario.

5.3 RESULTS

1. Scenario: Response to different fishing pressures on pelagic fish

When fishing pressure on pelagic fish was altered in the system, the most rapid response was among the target species, with changes in biomass over time (Fig 5.1). Indirect

responses of other groups (seabirds) in the system occurred over larger time scales (5 years).

a) MSY scenario

Under the MSY scenario (Fig. 5.1a) the application of constant fishing mortality (F = 0.25) for pelagic fish from 2015 resulted in an overall increase in seabird biomass (Fig. 5.2a). Offshore divers showed the most striking increase in total biomass of (77.8 %). Offshore-surface feeders also benefited: their biomass increased by 19 % after 20 years (Fig. 5.2a), but gull biomass was less responsive, increasing by 5% up to 2035 (Fig. 5.2a).

b) "Status quo" or *no change scenario*

Under the no-change scenario (Fig. 5.1b), the application of low fishing mortality for pelagic fish from 2015 resulted in an overall increase in seabird biomass (Fig. 5.2b). After 20 years offshore divers showed a remarkable increase in total biomass of 100%, while offshore surface feeders increased their biomass by 21.34 % (Fig. 5.2a). Gull biomass changed little over time increasing only by 5.09% (Fig. 5.2b).

c) High fishing impact followed by a no-take scenario

Under the high fishing impact and no-take scenario (Fig. 5.1c) there was initially an exponential decline in the biomass of offshore divers, with an overall decline in their biomass of 89.8 % by 2025 (Fig. 5.2c); however over the following 10 years this functional group experienced a small recovery (after a complete cessation of fishing from 2025 to 2035). Offshore-surface feeders showed a slight initial decline, but the final biomass had increased by 21.2% compared with the starting value (Fig. 5.2c). Gull biomass once again changed very little under this scenario (Fig. 5.2c).

2. Scenario: discard ban

Following a ban in the production of discards there was a decline of 51.02% in the biomass of gulls in comparison to the situation when discards were kept in the model. As a secondary effect of gull decline, seabird offshore divers increased their biomass by 32.77 %. Seabird offshore surface feeders did not exhibit any particular change in either scenario (discards on and off; Fig. 5.3a). Similar results were obtained when the same scenario was run including some behavioral adjustments (such as increasing the potential foraging time of seabird groups; Fig. 5.3b); however in this case gulls were less impacted with a biomass decline of 26.47%.

3. Scenario: effect of increasing sea temperature

Under the increasing sea temperature scenario (Fig 5.4a), all groups' biomass declined in the system by 2025; however, seabird groups showed different responses, with offshore surface feeders' biomass declining by 30.39%, offshore divers by 42.08 % and gulls by 53.2 %.

4. Scenario: response to combining fisheries and climate variation

The combination of the indirect effects of climate variation and a 50% reduction in fishing effort from 2015 to 2025 still showed an overall decline in the biomass of seabirds offshore surface feeders and gulls over time (Fig. 5.4b), with declines in the biomass respectively of 29.56% and 73.18%. Offshore divers biomass initially declined by 22% in 2010, however when the fishing was reduced of 50% (2015-2025) this value increased by 28.62%.

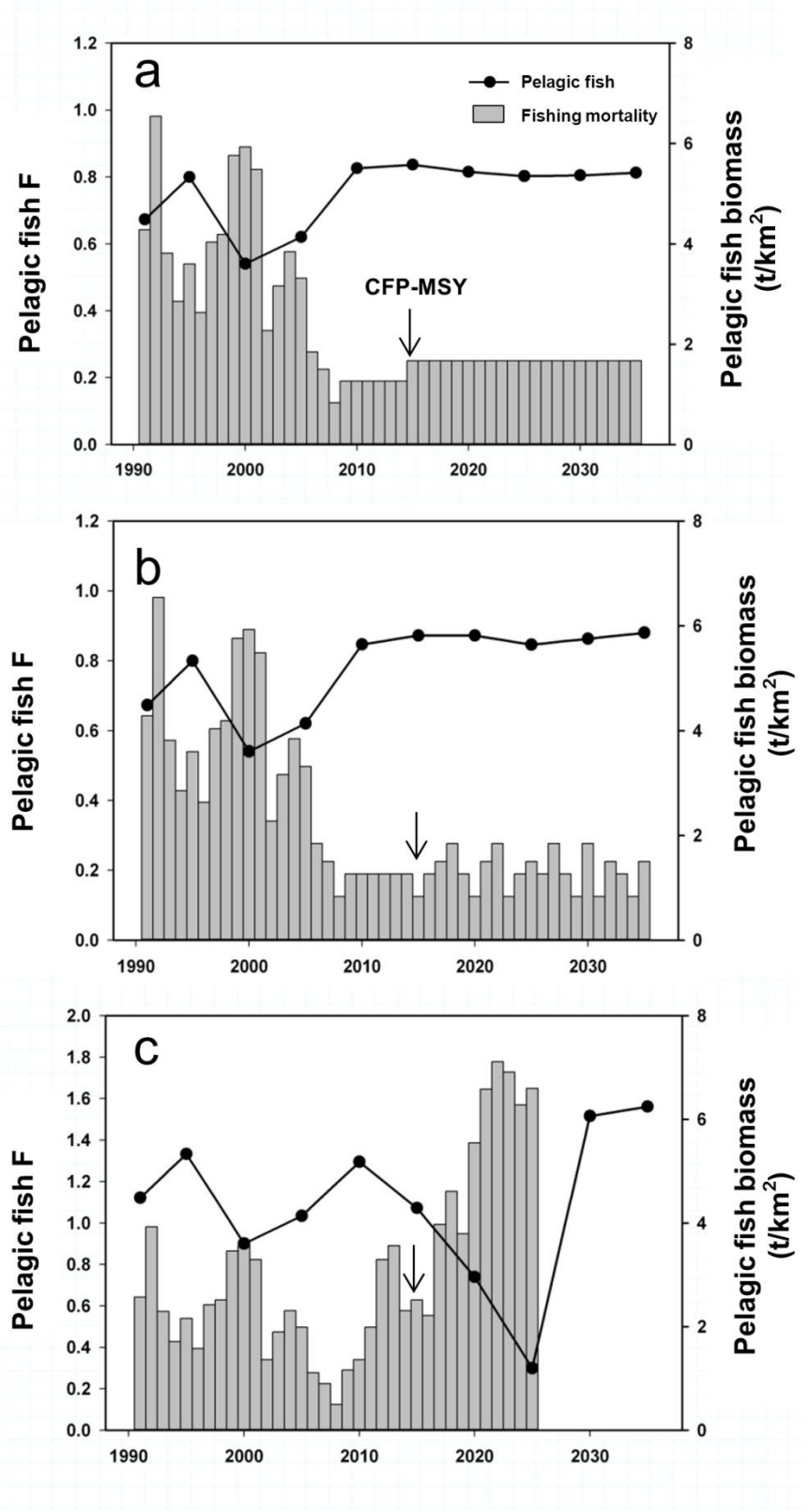

Figure 5.1 Simulated scenarios of changing fishery mortality (F) of pelagic fish and predicted effects on their relative biomass. The arrow refers to 2015 when the reform of Common Fishery Policy (CPF) will enter into force. (a) Application of Maximum Sustainable Yield (MSY): the largest yield (or catch) that can be taken from a species' stock over an indefinite period. (b) Simulation of no changes in fishery pattern over time. (c) Increase of F over time followed by no-take ban from 2025

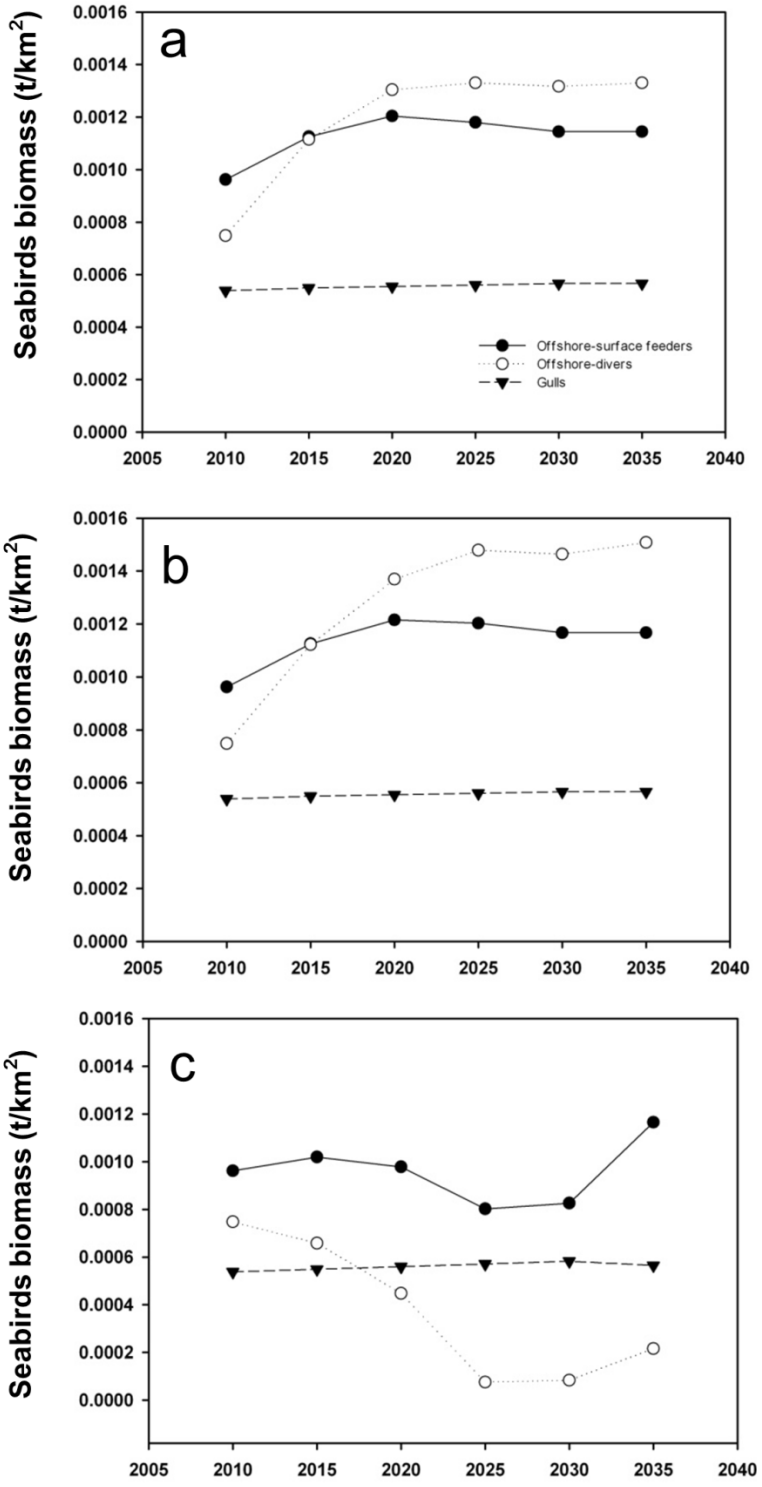

Figure 5.2 Response of seabird groups to direct effects of simulated changes in pelagic fish fishery mortality (F) as outlined in Figure 1. (a) Application of Maximum Sustainable Yield (MSY). (b) Simulation of no changes in fishery pattern over time. (c) Increase of F over time followed by no-take ban from 2025. Seabird offshore-surface feeders includes: northern gannet, black-legged kittiwake and northern fulmar; Seabird offshore divers includes: common guillemot, Atlantic puffin and razorbill; Gulls includes: lesser black backed gull, herring gull, great black backed gull, and black headed gull.

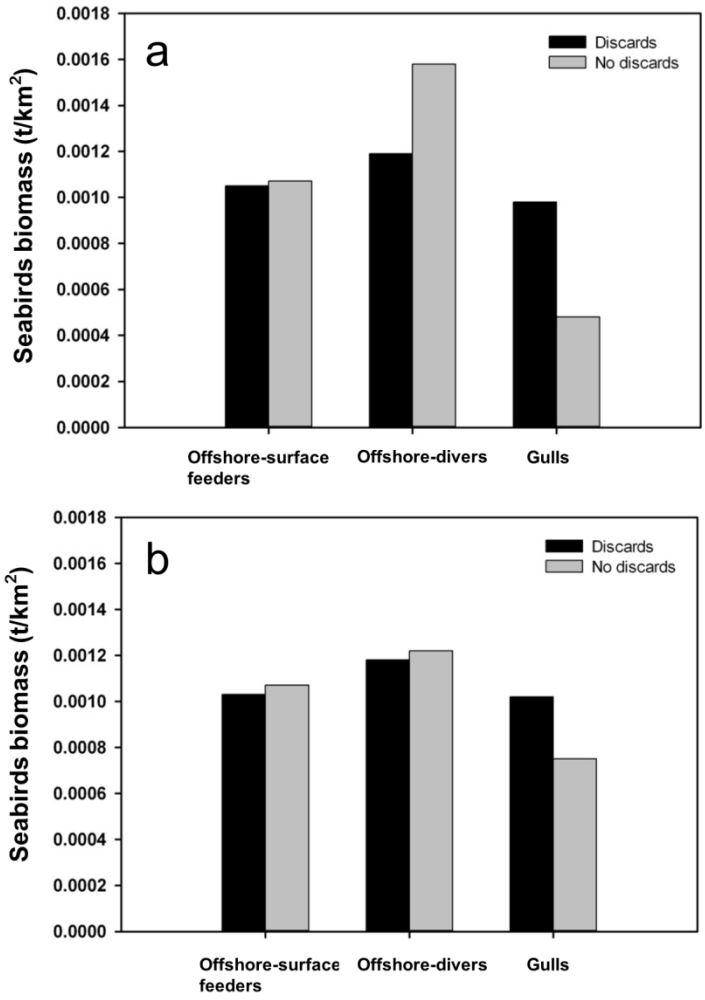

Figure 5.3 Effects of cessation of discarding on seabird biomass in the Celtic Sea estimated from Ecosim model. (a) Seabird biomass change following a discard ban. (b) Seabird biomass change following a discard ban, but with model including increasing seabird foraging time. Biomass values for FGs were recorded at 2020.

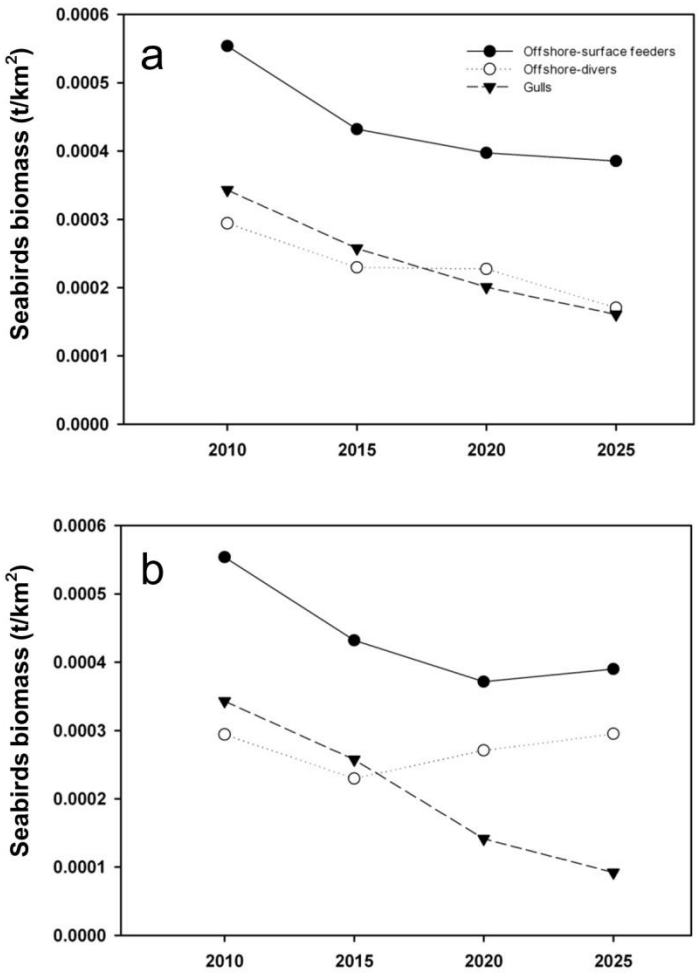

Figure 5.4 Seabirds response to climate forcing on Primary Production (PP). (a) Only changes to PP are applied while fishery is kept at constant value. (b) Both climate and fishery are modified; in particular fishery effort is reduced of 50% from 2015.

5.4 DISCUSSION

The results of the Ecosim model simulations show that predicted changes in fisheries management and climatic conditions are likely to greatly impact the biomass of seabirds in the Celtic Sea, with quite different responses from the three separate foraging guilds (Figs. 5.2-5.4). Although the findings here are consistent with previous studies showing that fisheries and climate change can have profound impacts on apex predators such as seabirds (Frederiksen et al., 2004a, Rolland et al., 2010); our results suggest that in the Celtic Sea climate forcing and fishery both play a crucial role on seabirds. Moreover, there is some evidence that the impact of climate change might outweigh the effect of changing fishing practices.

To our knowledge this represents the first study to show the potential interacting effects of future climate and fisheries scenarios on marine apex predators by using a complex ecosystem-based approach. Possible mechanisms and explanations for these findings are discussed below.

Direct fisheries effects on seabirds and their trophic relationships

Small shoaling pelagic fish are an important prey of seabirds and these are the target of industrial fisheries for the production of fishmeal and oils (Furness, 2003). It is, therefore, unsurprising that removal of large quantities of these fish by industrial fisheries may deleteriously impact upon seabird communities (Furness and Camphusyen, 1997). Our Ecosim model was consistent with this, showing that pelagic fish play a key role in altering seabird biomass in the Celtic Sea; however, our fishing scenarios (Fig.5.1) had greatly differing impacts on seabird foraging guilds (Fig. 5.2).

The current CFP reform (EU, COM 2009) proposed the application of fishing mortality values associated with the MSY. The application of the fishing mortality rate for pelagic fish in the Celtic Sea ecosystem predicted an overall positive effect on seabirds (Fig.

5.2a); in particular offshore divers (puffins, razorbills and common guillemots) showed the highest increase in their biomass in the ecosystem because of the importance of these fish species in their diet compared to other seabird groups (i.e. gulls and surface feeders). The application of MSY to commercially important fish species has been acknowledged as good practice, because it will minimize fisheries impacts at the ecosystem level (Hilborn, 2011), although this is still under debate (Bellido et al., 2011).

Currently, very little is known about future ecosystem responses to the application of the proposed CFP reform, and it is possible that fishing trends could continue as before if there is a delay in the implementation of reforms (Fig. 5.1b). If this is the case, it is likely that offshore divers and offshore-surface feeding seabirds will not suffer food shortages, as a result of low fishing impact on pelagic fish (Fig. 5.2b). Fishery effects on seabird communities have been well documented in the North Atlantic (Barret and Krasnov, 1996; Carscadden et al., 2002). Our results describe the possible future impacts upon pelagic fish and the relative trophic effects upon associated apex predators that could occur if fishing pressure remains in line with current trends in the Celtic Sea (ICES, 2010).

The need to produce long-term sustainability of marine fisheries resources and biodiversity as a whole has been highlighted in the Marine Strategy Framework Directive (2008). Management plans require taking account of fish stocks and the effect on species associated with or dependent upon harvested species (Bellido et al., 2011). Restoring fish populations would lead to the restoration of associated or dependent species before their populations also become endangered. This is very important for seabirds that are vulnerable to food shortages, especially during the breeding season (Aebischer et al., 1990). In a high fishing impact and then no-take scenario (Fig. 5.1c) we simulated the potential effects of high fishery mortality associated with the establishment of a no-take ban after 10 years of pelagic fish overexploitation. The

reason behind this is that the Celtic Sea fisheries that target pelagic fish species are currently expanding (Pinnegar et al., 2002) and if they are not sustainably managed pelagic fish stocks may be rapidly overexploited. There is growing attention, therefore, in designating no-take zones (EU, 2008) as an approach to fishery management that maintains the structure and functioning of marine ecosystems (Lubchenko et al., 2003). Robb et al. (2011) suggested that no take MPAs, in which all fishing is prohibited, can result in greater productivity of fish stocks; this is likely to have a positive effect on the highest trophic levels, notably on seabirds. Our results predict that seabirds would recover after the designation of a no-take zone (Fig. 5.2c) following a period where the fishing effort on pelagic fish species was particularly high (Fig. 5.1c). Such a recovery after strong top-down control on the food web, in particular on small pelagic fish, has already been demonstrated for apex predators in the North Sea (Furness, 2003).

Indirect fisheries effects on seabirds: application of a discard ban

The simulation of the discards ban on the Celtic Sea ecosystem predicted a decline in scavenger seabird biomass, in particular of gulls and offshore-surface feeders (where the latter includes black-legged kittiwakes, northern fulmars and northern gannets). As a secondary effect of the decline in gulls, seabird offshore divers increased in biomass (Fig. 5.3a). This result is in contrast with previous findings where large scavenging seabirds, unable to find sufficient discards, have turned to predation on smaller seabirds to supply their dietary requirements (Phillips et al., 1999). Similar results were obtained when the same scenario was run including some behaviour adjustments (such as increasing the potential foraging time of seabird groups; Fig. 5.3b). Our results suggest possible trophic mechanisms that may occur in the food web; however such effects may be confounded by the fact that scavengers can also feed on alternative prey such as small, shoaling, lipid-rich species, for example, lesser-sandeel *Ammonydes marinus* and capelin *Mallotus villosus* (M.) (Pearson, 1968; Barret and Kransov, 1996). At this stage

it is necessary to analyse all possible options, but more research needs to be undertaken in order to include these effects in ecosystem-based management plans (Bellido et al., 2011).

Climate effects (bottom-up) and seabirds' trophic response

The current climate change scenarios for the Celtic Sea predict a tendency for stratification as a result of increasing Sea Surface Temperature (SST) (MCCIP, 2010). Environmental changes (increasing SST) have been shown to have dramatic effects from plankton communities (Richardson and Shoeman, 2004) up to the highest trophic levels (Hunt et al., 2002; Gremillet et al., 2008b). Our scenario predicts a general decline of all ecosystem components in response to an increase in winter SST. In particular, seabird groups are likely to be affected (Fig. 5.4a), showing a decline in their biomass mediated by bottom-up effects.

Combined climate (bottom-up) and fisheries (top-down) effects on seabirds

When climate change effects (bottom-up control) were combined with fishing impacts (top-down control), the model predictions showed an overall decline in the biomass of offshore surface feeders and gulls, while seabird offshore divers increased with reduced fishing effort (Fig. 5.4b). Our results suggest that climate impacts may outweigh fisheries effects for some seabirds, and, in this case, even a reduction in the fishing effort (reduced from 2015 by 50%) does not have any positive effect upon the food web. This result could be explained by the fact that seabird groups which feed upon discards (gulls and offshore surface feeders) would be negatively impacted by the reduction of prey availability, in response to bottom-up effect as well as decrease of an alternative food source (discards). Some studies suggest that marine ecosystems under intense exploitation could evolve towards bottom-up control with greater sensitivity to climate forcing; however, climate effects are not likely to have immediate impacts on marine systems as they occur slowly (Perry et al., 2010). Our scenario shows that despite a 50%

reduction in fishing effort some of the ecosystem components declined in response to a strong bottom-up effect. This prediction suggests the urgent need to apply lasting schemes for the management of fisheries in the Celtic Sea as it is unknown what impact the climate will have in the future, and the current lack of solid planning with regard to fisheries could cause severe disruption to the stability of the ecosystem (Planque et al., 2010).

5.5 CONCLUSIONS AND RECOMMENDATIONS

The Ecosim approach can be a valuable tool for ecosystem-scale adaptive management experiments and here it has helped to elucidate possible trophic mechanisms in response to future fishing and climate impacts in the Celtic Sea. The results of this study could have implications for both management plans and conservation policy; in fact our simulations have demonstrated that seabird populations are vulnerable to both fishery and environmental change, and that climate change in the future may have the greatest effect on some components of the ecosystem. The results of this study meet the need to consider the additive effects of climate variation and fisheries (Planque et al., 2010).

Our simulations have demonstrated that seabirds are able to recover from human impacts, although the rate of this recovery is subject to the configuration of the model, and particularly on the vulnerability values assumed. It must be remembered that in the present study we have only examined particular combinations of Ecosim settings for each scenario; however the seabird responses were consistent under different vulnerability values. Nevertheless it is challenging to predict an ecosystem's response to future fishing and climate forcing. In many instances the model predictions were consistent with other studies' results suggesting that the model is capable of describing

seabird response to natural and anthropogenic impacts and the future projections could be taken into account for biodiversity management plans.

Chapter 6

Discussion and Conclusions

In this thesis the effects of climate change and fisheries on the Celtic Sea ecosystem are evaluated, in particular focussing on the response of seabird populations. In the following discussion the main findings of each chapter are summarised and discussed in a wider context.

Marine ecosystems versus climate change

Human-induced climate change and fisheries have profoundly impacted marine ecosystems across the globe, resulting in long-term threats to biodiversity (Pauly et al., 2005; Planque et al., 2010; Guldberg and Bruno, 2010). In addition the high degree of spatial heterogeneity in marine ecosystem response to climate and fisheries impacts (Halpern et al., 2008; Beaugrand et al., 2009, McGinty et al., 2011) have highlighted the need for more research at the regional scale. Around the British Isles one of the most studied ecosystems is the North Sea; this region has been strongly impacted by climate change and fisheries with dramatic changes in the ecosystem structure (Aebischer et al., 1990; Beaugrand, 2004; Frederiksen et al., 2004a, 2006). However, marine ecosystems are not equally sensitive to climate change or fisheries impacts, and are likely to respond to variations in different ways according to their own history and resilience. For this reason we focussed our study on the Celtic Sea, an important and less studied marine ecosystem of the Great Britain continental shelf.

The aim of **Chapter 2** was to research the effects of climate change on the pelagic food web in the Celtic Sea. Using long-term data, we examined possible direct and indirect 'bottom-up' climate effects across four trophic levels, focussing on the response of four seabird species breeding at Skomer. Our results showed both direct and indirect effects of climate change on the Celtic Sea food web, suggesting a weak climate impact from

mid-trophic levels to seabirds. Despite previous studies having linked climatic conditions and seabird demographics in this region (Votier et al., 2005, 2008, 2009; Riou et al., 2011), the role of climate change on the Celtic Sea remains unclear, but it certainly does not appear to share the same very strong signal exhibited elsewhere in the North Atlantic (i.e. North Sea). A possible explanation could be that the North Sea has experience a strong reorganisation of the zooplankton community over the last decades in response to the increase of SST, leading to a northward expansion of warm-water copepod species *Calanus helgolandicus* (low lipid) and a decline in cold-water zooplankton *Calanus finmarchicus* (G.) (high lipid) (Beaugrand et al., 2002; Beaugrand, 2004). As a consequence of this establishment of warm water conditions, primary and secondary productivity were dramatically modified (Beaugrand et al., 2002) forcing a bottom-up control on the trophic food web. As a result of this shift the availability and quality of small pelagic fish were drastically reduced affecting seabird reproductive performance (Mavor et al., 2005; Wanless et al., 2005; Frederiksen et al., 2006). In the Celtic Sea the zooplankton community is largely dominated by the warm-water copepod species *Calanus helgolandicus* (Planque and Fromentin, 1996), and as a consequence pelagic fish here might habitually feed on low lipid zooplankton, whereas fish in the North Sea are more likely to feed on high lipid prey; a change in zooplankton would, therefore, be more likely to have a striking impact in the North Sea ecosystem compared with the Celtic Sea.

In this study we also investigated the specific response of four seabird species to direct and indirect climate change effects, the rationale behind this choice is the different ecology and different trends in population demography occurring over the last two decades. For example, while black-legged kittiwake (*Rissa tridactyla*) numbers have decreased significantly, the numbers of the three Alcids (common guillemot *Uria aalge*, razorbill *Alca torda* and Atlantic puffin *Fratercula artica*) have increased, highlighting

the need to investigate which driving force was causing these different population changes. This study could be further developed by combining datasets across seabird species using e.g. multivariate statistics, in order to develop integrative indicators of the marine ecosystem status. This approach has been applied in the North Sea where a general seabird index of breeding performance was created and correlated with changes in food availability (Frederiksen et al., 2007c). Combining long-term data across multiple trophic levels can allow full description the marine ecosystem and evaluation of its response to changing environmental conditions. However, we believe that species-specific studies of seabird productivity are fundamental to understand species ecology, and should be combined with broader indices in order to inform biodiversity conservation.

Beaugrand et al., (2008) showed that different marine ecosystems of the Northeast Atlantic are not equally sensitive to climate change, and some regions are more vulnerable to changing temperatures (i.e. North Sea). These findings emphasised the necessity of region-wide research looking at long-term response of marine ecosystems to climate change impacts at multiple trophic-levels. In **Chapter 3** we have furthered the previous study and tested for long-term climate-related influences and regional variability by using a multiple-trophic level approach in three marine systems in southwest Britain: the Irish Sea, the Celtic Sea and the English Channel. This time one seabird species (black-legged kittiwake) was used as an indicator of the health of the ecosystem in function of changes of food availability (fish larvae abundance). This study demonstrated that the response to climate change across three regions (Irish Sea, Celtic Sea and English Channel) in Great Britain is broadly similar and, despite the overall increase in SSTs in the North Atlantic (Edwards et al., 2006), there is no evidence of a bottom-up signal across four trophic levels. However, small-scale regional differences in food availability affecting kittiwake productivity during the study period

were found in one colony in the Irish Sea but not in the others. In the Celtic Sea for example, kittiwake productivity at Skomer does not seem to be influenced by changes in food availability, this result was consistent either when small size herrings were used as a food proxy (Chapter 2) or fish larval abundance (Chapter 3).

This finding highlighted the need to further investigate the possible impact of other cues (i.e. fisheries or predation) which are likely to explain the current decline of kittiwakes in the southwest of Great Britain (Brown et al., in prep). This study could be further developed by modelling fisheries or predation effects but unfortunately long-term fisheries data (e.g. ICES) on small pelagic fish (lesser sandeel *Ammodytes marinus*, sprat *Sprattus sprattus* and herring *Clupea harengus*) did not exist, or were not consistent for all three regions; however, we believe that similar information may be available, although only for limited time period, from fishery-independent surveys (i.e. CEFAS).

Information regarding possible predators (i.e. gulls) was available only for some of the kittiwake colonies in the south west of Great Britain from the Seabird Monitoring Programme, but was not consistent in the three regions. The application of spatial-temporal multiple-trophic level modelling is a valid approach which can improve our understanding of how different marine ecosystems respond to changes. One of the main limitations of this type of approach is data availability as very often long-term datasets relative to different trophic levels are scarce. Studies have applied similar approaches covering only a few trophic levels (Carscadden et al., 2002; Diamond and Devlin, 2003; Durant et al., 2003; Österbloom et al., 2006), and despite their important contribution to improving our general understanding of the climate impacts on marine ecosystems, information is still missing and further investigation is required using detailed datasets.

Ecosystem-based approach and its implications: where are we going from here?

In recent years, marine ecosystem management has been revolutionised by the application of ecosystem-based approaches such as that offered by Ecopath with Ecosim. This approach offers great flexibility including the ability to investigate the potential synergistic effects of fisheries and climatic impacts (Garcia et al., 2003; EU COM, 2009). Of particular interest is the combination of such a complex approach and biodiversity protection, as, in most cases, fisheries management plans do not take into consideration that fish species are also exploited by natural marine predators such as fish top-predators, seabirds and marine mammals. The need to use complex ecosystem models to describe trophic relationships within the marine environment, and test for fisheries-induced indirect effects focussing on seabird response has been pointed out in the past (Frederiksen et al., 2007b). Complex tropho-dynamic models such as 'Ecopath with Ecosim' (EwE, Christensen and Walters, 2004) or size-spectra models 'Osmose' (Shin and Cury, 2001) represent powerful tools to investigate trophic relationships among species in detail.

In **Chapter 4** an Ecopath model was used to describe the Celtic Sea trophic food web. The application of such a complex model represents an important attempt to integrate the available biological data for the Celtic Sea into a coherent format, in order to give a comprehensive ecosystem description that can be used to support future studies and management plans. This study described the Celtic Sea food web and trophic structure, and also showed the importance of some key prey species for seabirds and their trophic interactions. The results of this study can be used to support future biodiversity conservation schemes and facilitate policy-making decisions for the whole Celtic Sea food web.

The Ecosystem-based approach developed in the previous study was further developed in **Chapter 5** by the application of the dynamic model Ecosim. In this study some of the future fisheries management schemes suggested by the Common Fisheries Reform (EU COM, 2009) combined with climate change scenarios were tested by evaluating changes in seabird biomass. The findings of this study suggest that changes in fisheries management and climatic conditions are likely to greatly impact seabirds in the Celtic Sea, with quite different responses from the seabird groups under diverse scenarios. Our model predictions were consistent with other studies' results (Frederiksen et al., 2004a, Rolland et al., 2010) suggesting that the model is capable of describing ecological mechanisms and can be used as support for future biodiversity management plans. This study established the collaboration with John Pinnegar and Steve Mackinson (CEFAS, UK); the results of the Ecopath model presented in this study completed the application of such models to British waters (prior to this North Sea, Irish Sea, English Channel models were created). These results are going to be used in a DEFRA-CEFAS project in order to define fishery guidelines for Great Britain waters using an ecosystem-based approach. The study is going to be further developed by the application of the spatial planning tool Ecospace (belonging to the Ecopath with Ecosim software) for the Celtic Sea region. Currently there is growing attention in designating Marine Protected Areas (MPAs) as part of the Natura 2000 network following the Habitats and Birds Directives (92/43/EEC) (EU, 1992) and later the Marine Strategy Framework Directive (2008/56/EC) (EU, 2008). This intense interest in the implementation of MPAs is due to increasing evidence of this being a robust approach to habitat and biodiversity conservation, fisheries management, and maintaining ecosystem structure (Lauck et al., 1998, Lubchenko et al., 2003). Growing attention is now being given to the use of MPA networks for seabird conservation (Kober et al., 2010) and the application of the Ecospace approach could help the process of identification of important pelagic habitats

for seabirds in the Celtic Sea region, with particular relevance to future changes in fishery regimes and climate conditions.

In summary, the research reported here represents the first study to focus upon ecosystem response to climate and fisheries impacts in the Celtic Sea, over multi trophic levels. Research findings clearly highlight the potential benefits of applying of a complex ecosystem-based approach across a range of spatial and temporal scales to support management decisions. The application of Ecopath with Ecosim offers an opportunity to forward knowledge and understanding of anthropogenic impacts upon marine ecosystems and, coupled with Ecospace, can provide key decision support for future marine management and conservation policy.

APPENDIX 1

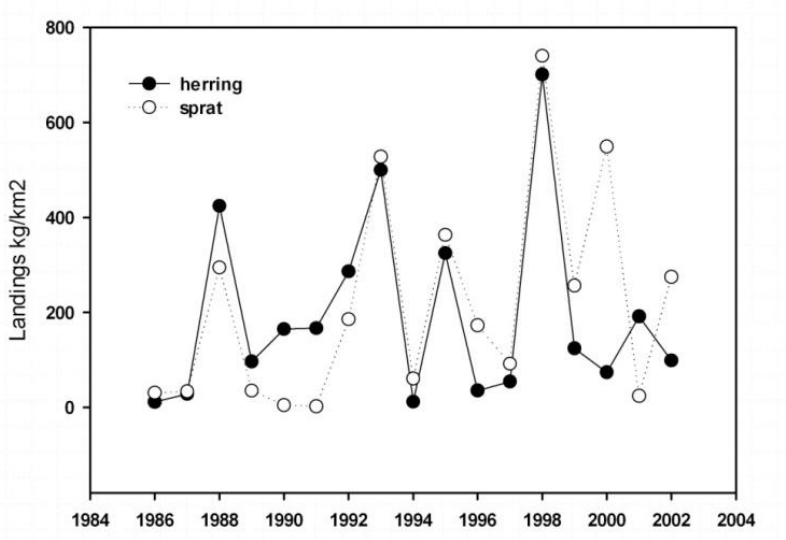

Figure A1.1 Herring and sprat landings (kg/km^2) from the Western and Celtic Sea Ground Fish Survey (WCGFS) (CEFAS). This trawl survey is designed to study the distribution, composition and abundance of all fish, commercial shellfish and cephalopod species in the Celtic Sea. Pearson's coefficient of correlation: 0.715, p value= 0.001.

Table A1.1 Correlation matrix (Pearson's coefficient) between covariates. Significance is indicate as follow: pvalue< 0.001 ***, pvalue,< 0.01**, pvalue<0.05* SNAO: spring North Atlantic Oscillation index; WNAO: winter North Atlantic Oscillation index; SSST: spring Sea Surface Temperature; WSST: winter Sea Surface Temperature; Small cop: small copepods (<2mm); Large cop: large copepods (>2mm); KittBS: black-legged kittiwake productivity; GuiBS: guillemot productivity; RazBS: razorbill productivity; PufBS: puffin productivity; Her 0-g: herring 0-group; Her-1g: herring 1-group; Large cop: large copepod; Small cop: small copepods; KittRt: black-legged kittiwake population growth rate; GuiRt: guillemot population growth rate; RazRt: razorbill population growth rate; PufRt: puffin population growth rate.

	Year	Diatom	SNAO	WNAO	SSST	WSST	Kitt BS	Guil BS	Raz BS	Puf BS	Herr 0-gr	Herr 1-gr	Large cop	Small cop	Kitt Rt	Gui Rt	Raz Rt	Puf Rt
Year	1.00																	
Diatom	0.36	1.00																
SNAO	-0.22	0.18	1.00															
WNAO	-0.22	0.09	**0.43 ***	1.00														
SSST	**0.58 ****	0.26	-0.23	0.21	1.00													
WSST	**0.66 *****	-0.001	-0.12	0.17	**0.85 *****	1.00												
Kitt BS	-0.08	0.05	-0.22	0.13	-0.19	-0.13	1.00											
Gui BS	**-0.59 ****	**-0.46 ***	-0.06	0.16	-0.09	-0.08	-0.04	1.00										
RazBS	**-0.53 ***	**-0.55 ***	-0.49	0.09	0.08	0.03	-0.01	**0.69 ****	1.00									
Puf BS	-0.20	**-0.52 ***	-0.01	-0.18	**-0.50 ***	-0.14	0.13	0.08	0.11	1.00								
Herr 0-gr	-0.27	-0.01	0.10	0.31	-0.22	-0.18	0.22	0.01	0.21	0.16	1.00							
Herr 1-gr	-0.21	0.23	-0.34	-0.19	-0.25	-0.24	0.15	-0.20	-0.20	0.08	-0.26	1.00						
Large cop	-0.12	-0.39	-0.29	-0.27	-0.36	-0.13	0.14	0.20	0.39	0.27	0.25	0.22	1.00					
Small cop	**-0.69 *****	**-0.49 ***	-0.14	0.04	-0.36	-0.32	0.13	**0.52 ***	**0.63 ***	0.33	0.29	0.20	**0.49 ***	1.00				
KittRt	0.00	0.26	**0.43 ***	0.23	0.04	-0.03	-0.17	-0.10	-0.04	-0.38	0.23	-0.41	-0.10	-0.03	1.00			
GuiRt	-0.03	0.06	0.29	-0.15	0.13	-0.03	-0.42	0.03	0.12	-0.37	-0.11	-0.43	-0.17	-0.16	0.22	1.00		
RazRt	0.10	0.27	0.19	0.02	0.03	-0.15	-0.18	-0.29	-0.07	-0.35	-0.11	-0.41	-0.28	-0.20	0.11	0.37	1.00	
PufRt	-0.12	0.17	-0.05	-0.20	0.23	-0.12	-0.32	-0.05	0.04	-0.20	0.07	0.00	-0.20	0.15	0.22	0.42	0.23	1.00

Table A1.2 Competing models for low trophic levels. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; Significant relationships are highlighted in **bold,** not significant variables included in the model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
				Diatom			
WSST + year	0.28	3	22	4.59	0.16	WSST 0.11 **year 0.02**	WSST -0.362 (±0.221) **year 0.054 (±0.022)**
year	0.25	2	22	5.24	0.09	0.09	0.03 (±0.01)
				Small copepods			
diatom + year	0.30	3	22	1.71	0.47	diatom 0.115 **year 0.003**	diatom -0.22 (±0.13) **year -0.03 (±0.01)**
year	0.26	2	22	1.96	0.43	**year <0.001**	**year 0.04 (±0.01)**
				Large copepods			
diatom + WNAO	0.24	3	22	2.16	0.19	diatom 0.08 WNAO 0.10	diatom -0.250 (±0.13) WNAO -0.101 (±0.06)
WNAO	0.16	4	22	2.53	0.09	WNAO 0.09	WNAO -0.111 (±0.06)

Table A1.3 Competing models for mid trophic levels. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; 2lag-SSST: 2 years lagged spring Sea Surface Temperature; large cop: large copepods (>2mm); significant relationships are highlighted in **bold**, not significant variables included in the model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
			Herring 0-group				
1lag-SSST + WNAO	0.20	3	22	4.00	0.25	**1lag-SSST 0.02** WNAO 0.11	**1lag-SSST -0.450 (±0.180)** WNAO 0.133(±0.081)
1lag-SSST	0.18	2	22	4.57	0.19	**0.02**	**-0.463 (±0.188)**
			Herring 1-group				
2lag-SSST	0.24	2	22	4.60	0.15	**0.04**	**-0.41 (±0.19)**
2lag-SSST + large cop	0.09	3	22	4.44	0.13	2lag-SSST 0.08 large cop 0.43	2lag-SSST -0.37 (±0.20) large cop 0.001(±0.002)

Table A1.4 Competing models for apex predators. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, and high values indicate strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. WNAO: winter North Atlantic Oscillation index; SNAO: spring North Atlantic Oscillation index; WSST: winter Sea Surface Temperature; 1lag-SSST: 1 year lagged spring Sea Surface Temperature; her 0-g: herring 0-group; her-1g: herring 1-group; Significant relationships are highlighted in **bold**, not significant variables included in the model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
				Black-legged kittiwake			
Productivity							
intercept only	0.25	1	22	1.04	--	**<0.001**	
Population growth rate							
SNAO	0.32	2	22	0.07	0.16	**0.036**	**0.0314 (±0.014)**
SNAO + her 0-g	0.14	3	22	0.07	0.16	**SNAO 0.045** her 0-g 0.349	**SNAO 0.03 (±0.014)** her 0-g $0.575x10^{-7}$ ($\pm 0.6 x10^{-7}$)
				Common guillemot			
Productivity							
year	0.23	2	19	0.07	0.29	**0.009**	**-0.008 (±0.002)**
SNAO + her 1-g + year	0.12	4	19	0.05	0.38	SNAO 0.113 her 1-g 0.097 **year 0.003**	SNAO -0.028 (±0.017) her 1-g $-0.344x10^{-6}$ ($\pm 0.194x10^{-6}$) **year -0.009 (±0.002)**
her 1-g + year	0.12	3	19	0.07	0.31	her 1-g 0.261 **year 0.008**	her 1-g $-0.222x10^{-6}$ ($\pm 0.190x10^{-6}$) **year -0.008 (±0.002)**
SNAO + year	0.10	3	19	0.07	0.30	SNAO 0.319 **year 0.007**	SNAO -0.017 (±0.016) **year -0.008 (±0.002)**
Population growth rate							
her 1-g + year	0.45	3	22	0.07	0.12	**her 1-g 0.042** year 0.557	**her 1-g $-0.352x10^{-6}$ ($\pm 0.161x10^{-6}$)** year -0.001 (±0.002)
				Razorbill			
Productivity							
1lag-SSST + SNAO + her 1-g + year	0.83	5	19	0.02	0.82	**1lag-SSST 0.01** **SNAO <0.001** **her 1-g 0.003** **year 0.01**	**1lag-SSST -0.144 (±0.05)** **SNAO -0.074 (±0.013)** **her 1-g $-0.884x10^{-6}$ ($\pm 0.167x10^{-6}$)** **year -0.01 (±0.003)**
Population growth rate							
her 1-g	0.23	2	22	0.06	0.09	her 1-g 0.09	her1-g $-0.264x10^{-6}$ ($\pm 0.149x10^{-6}$)
her 0-g + her 1-g	0.15	3	22	0.06	0.13	her 0-g 0.288 **her 1-g 0.005**	her 0-g $-0.06x10^{-6}$ ($\pm 0.055x10^{-6}$) her1-g $-0.327x10^{-6}$ ($\pm 0.147x10^{-6}$)
				Atlantic puffin			
Productivity							
intercept only	0.28	1	20	0.08	--	**<0.001**	
Population growth rate							
intercept only	0.28	1	20	0.09	0.55	0.578	

APPENDIX 2

Table A2.1 Correlation matrix (Pearson's coefficient) between covariates for the Irish Sea. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Bard: black-legged kittiwake productivity at Bardsey colony; Kitt Great: black-legged kittiwake productivity at Great Ormes Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

	Year	Kitt Bard	Kitt Great	Cop	Diat	Fish larvae	WSST	SST annual
Year	1.00							
Kitt Bard	0.44	1.00						
Kitt Great	-0.38	0.35	1.00					
Cop	0.36	-0.07	-0.45	1.00				
Diat	0.13	-0.02	0.12	0.46	1.00			
Fish larvae	-0.10	0.41	0.36	0.21	0.37	1.00		
WSST	**0.75 *****	0.44	-0.05	0.11	0.24	-0.21	1.00	
SST annual	**0.81 *****	0.41	-0.15	0.24	0.32	-0.20	**0.89 *****	1.00

Table A2.2 Correlation matrix (Pearson's coefficient) between covariates for the Celtic Sea. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. KittEleg: black-legged kittiwake productivity at Elegug Stacks colony; KittSkom: black-legged kittiwake productivity at Skomer colony; KittDumn: black-legged kittiwake productivity at Dunmore East colony; KittRam: black-legged kittiwake productivity at Ram Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

	Year	Kitt Eleg	Kitt Skom	Kitt Dunm	Kitt Ram	Cop	Diat	Fish larvae	WSST	SST annual
Year	1.00									
Kitt Eleg	-0.36	1.00								
Kitt Skom	-0.16	0.44	1.00							
Kitt Dunm	**0.59 ***	0.26	0.23	1.00						
Kitt Ram	-0.28	0.26	0.14	-0.06	1.00					
Cop	0.25	-0.20	-0.35	0.33	-0.49	1.00				
Diat	0.41	0.23	0.01	0.44	0.10	-0.04	1.00			
Fish larvae	0.14	-0.24	-0.33	-0.11	-0.24	0.17	0.42	1.00		
WSST	**0.65 ****	-0.09	-0.04	0.52	-0.23	0.26	0.20	-0.01	1.00	
SST annual	**0.82 *****	-0.18	-0.01	0.52	-0.17	0.34	0.35	-0.02	**0.68 ****	1.00

Table A2.3 Correlation matrix (Pearson's coefficient) between covariates for the English Channel. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Durl: black-legged kittiwake productivity at Durlston Head colony; Cop: copepods; Diat: diatoms; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

.

	Year	**Kitt Durl**	**Cop**	**Diat**	**Fish larvae**	**WSST**	**SST annual**
Year	1.00						
Kitt Durl	0.44	1.00					
Cop	0.20	-0.02	1.00				
Diat	0.30	0.19	0.34	1.00			
Fish larvae	-0.03	0.24	0.27	**0.55 ***	1.00		
WSST	**0.61 ***	0.40	0.04	-0.06	-0.19	1.00	
SST annual	**0.79 *****	**0.64 ***	0.04	0.42	0.16	**0.58 ***	1.00

Table A2.4 Correlation matrix (Pearson's coefficient) between covariates in different regions. Significance is indicating as follow: *p* value <0.001 ***, *p* value <0.01**, *p* value <0.05*. Kitt Bard: black-legged kittiwake productivity at Bardsey colony; Kitt Great: black-legged kittiwake productivity at Great Ormes Head colony; Kitt Eleg: black-legged kittiwake productivity at Elegug Stacks colony; Kitt Skom: black-legged kittiwake productivity at Skomer colony; Kitt Dumn: black-legged kittiwake productivity at Dunmore East colony; Kitt Ram: black-legged kittiwake productivity at Ram Head colonycolony Kitt Durl: black-legged kittiwake productivity at Durlston Head colony; Cop: copepods; Diat: diatoms; flarvae: fish larvae; WSST: Winter Sea Surface Temperature (average December-March); SST annual: annual average Sea Surface Temperature.

	Year	Kitt Bard	Kitt Great	Irish cop	Irish diat	Irish flarvae	Irish WSST	Irish SSTa	Kitt Eleg	Kitt Skom	Kitt Dunm	Kitt Ram	Celtic cop	Celtic diat	Celtic flarvae	Celtic WSST	Celtic SSTa	Kitt Dur	Chan cop	Chan diat	Chan farvae	Chan WSST	Chan SSTa
Year	1.00																						
Kitt Bard	0.44	1.00																					
Kitt Great	-0.38	0.35	1.00																				
Irish cop	0.36	-0.07	-0.45	1.00																			
Irish diat	0.13	-0.02	0.12	0.46	1.00																		
Irish flarvae	-0.10	0.41	0.36	0.21	0.37	1.00																	
Irish WSST	**0.75 *****	0.44	-0.05	0.11	0.24	-0.21	1.00																
Irish SSTa	**0.81 *****	0.41	-0.15	0.24	0.32	-0.20	**0.89 *****	1.00															
Kitt Eleg	-0.36	0.10	0.55	-0.47	0.08	0.43	-0.04	-0.05	1.00														
Kitt Skom	-0.16	-0.36	0.16	-0.32	0.19	-0.04	-0.05	0.04	0.44	1.00													
Kitt Dunm	**0.59 ***	**0.56 ***	0.22	0.01	0.37	0.42	0.50	0.51	0.26	0.23	1.00												
Kitt Ram	-0.28	0.08	-0.02	-0.31	0.42	0.26	-0.11	-0.16	0.26	0.14	-0.06	1.00											
Celtic cop	0.25	0.35	0.34	0.49	0.32	0.42	0.13	0.13	-0.20	-0.35	0.33	-0.49	1.00										
Celtic diat	0.41	**0.61 ***	0.03	-0.15	-0.21	0.22	0.37	0.39	0.23	0.01	0.44	0.10	-0.04	1.00									
Celtic flarvae	0.14	0.15	-0.03	0.16	-0.41	-0.12	0.06	-0.03	-0.24	-0.33	-0.11	-0.24	0.17	0.42	1.00								
Celtic WSST	**0.65 ****	**0.62 ***	0.19	0.01	0.15	-0.19	**0.85 *****	**0.76 *****	-0.09	-0.04	0.52	-0.23	0.26	0.20	-0.01	1.00							
Celtic SSTa	**0.82 *****	0.46	-0.11	0.41	0.46	-0.03	**0.72 *****	**0.86 *****	-0.18	-0.01	0.52	-0.17	0.34	0.35	-0.02	**0.68 ****	1.00						
Kitt Dur	0.44	0.29	-0.04	-0.09	0.09	-0.17	**0.57 ***	**0.70 *****	0.15	0.19	0.18	-0.08	-0.25	0.48	-0.27	0.43	**0.56 ***	1.00					
Chan cop	0.20	**0.59 ***	0.16	-0.32	-0.34	0.16	0.06	0.06	0.21	-0.15	0.32	0.02	-0.05	0.43	0.18	0.28	0.00	-0.02	1.00				
Chan diat	0.30	0.29	-0.25	0.22	0.12	**0.54 ***	0.11	0.25	0.41	-0.11	0.42	0.19	0.03	**0.65 ***	0.02	-0.22	0.21	0.19	0.34	1.00			
Chan flarvae	-0.03	0.19	-0.03	0.07	0.04	0.35	-0.04	-0.02	0.32	-0.19	-0.06	0.27	-0.25	0.41	0.08	-0.22	0.10	0.24	0.27	**0.55 ***	1.00		
Chan WSST	**0.61 ***	0.46	0.37	-0.07	0.41	0.15	**0.83 *****	**0.61 ***	0.14	0.15	**0.75 ****	0.05	0.22	0.20	-0.23	**0.79 *****	0.51	0.40	0.04	-0.06	-0.19	1.00	
Chan SSTa	**0.79 *****	**0.61 ***	0.07	0.10	0.43	0.21	**0.78 *****	**0.84 *****	0.18	-0.02	**0.62 ***	0.17	0.22	0.51	-0.39	**0.61 ***	**0.88 *****	**0.64 ***	0.04	0.42	0.16	**0.58 ***	1.00

Table A2.5 Competing models for the Irish Sea. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. 1lag-SST: 1 year lagged annual Sea Surface Temperature; Significant relationships are highlighted in **bold**; not significant variables included in the model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS							
Diatom abundance							
Intercept only	0.47	1	17	1.04		<0.001	4.717 (±0.06)
PRIMARY CONSUMERS							
Copepod biomass							
diatom	0.31	2	17	8.14	0.16	0.062	0.121×10^{-6}
Intercept only	0.18	1	17	10.33		<0.001	0.879 (±0.195)
Fish larval abundance							
Intercept only	0.26	1	17	2.29		<0.001	0.626 (±0.091)
APEX PREDATORS							
Black-legged kittiwake productivity							
Bardsey							
fish larvae + year	0.28	3	16	1.39	0.38	**fish larvae 0.022** **year 0.018**	0.604 (±0.233) 0.048 (±0.0.17)
fish larve lag + SSTa lag	0.12	3	16	1.55	0.31	fish larvae lag 0.054 **SSTa lag 0.039**	0.502 (±0.237) 0.483 (±0.211)
Great Ormes Head							
Intercept only	0.20	1	17	1.00		<0.001	0.500 (±0.060)

Table A2.6 Competing models for the Celtic Sea. AICc weight: Akaike's Information Criteria (corrected) weights, values range from 0 to 1, high values indicating strong support for a given predictor; k: number of parameters in the model; R^2: Adjusted coefficient. Significant relationships are highlighted in **bold**; not significant variables included in the model are also presented.

Model selected	AICc weight	k	n years	Deviance	R^2	p-value	Slope (±Standard Error)
PRIMARY PRODUCERS							
Diatom abundance							
year	0.42	2	17	2.45	0.12	0.098	0.035 (±0.020)
PRIMARY CONSUMERS							
Copepod biomass							
Intercept only	0.44	1	17	1.83		<0.001	1.115 (±0.082)
Fish larval abundance							
diatom	0.29	2	17	3.93	0.12	0.097	0.526 (±0.297)
Intercept only	0.26	1	17	4.76		<0.001	0.734 (±0.132)
APEX PREDATORS							
Black-legged kittiwake productivity							
Skomer							
Intercept only	0.24	1	17	0.88		<0.001	0.682 (±0.056)
Elegug Stacks							
Intercept only	0.20	1	17	0.096		<0.001	0.091 (±0.018)
Dunmore East							
fish larvae lag + year	0.38	3	17	0.434	0.41	fish larvae lag 0.07 **year 0.008**	-0.172 (±0.089) 0.026 (±0.008)
year	0.29	2	17	0.550	0.30	**0.012**	0.026 (±0.009)
Ram Head							
Intercept only	0.35	1	13	0.860		<0.001	0.442 (±0.074)

APPENDIX 3

Basic input parameters and data sources for the construction of the Ecopath model

1. Baleen whales

The SCANS II report (Hammond et al., 2006) recorded a density for minke whales *Balaneoptera acutorostrata* (L.) of 0.012 (animals/km^{-2}) in the Celtic Sea in 2005. Average weight was estimated to be 5.251 t (Sigurjonsson and Vikingsson, 1997), and baleen whale biomass was therefore estimated to be 0.0630 t km^{-2} using the equation:

Biomass (t km^{-2}) = abundance x average body weight (t) / area of the Celtic Sea (222,665 km^{2})

Equation 1

We assumed a Q/B y^{-1} value of 6.323 based on the average food consumption of minke whales, estimated from Sigurjonsson and Vikingsson (1997). A P/B y^{-1} value of 0.02 given in Trites et al. (1999) was also used. Diet is based on pelagic fish 99% and mackerel 1% (Pierce et al., 2004).

2. Toothed whales

Toothed whales include harbor porpoises *Phocoena phocoena* (L.) and several species of dolphin: the common dolphin *Delphinus delphis* (L.), white-beaked dolphin *Lagenorhynchus albirostris* (G.), white-side dolphin *Lagenorhynchus acutus* (G.), and bottlenosed dolphin *Tursiops truncatus* (M.). Harbour porpoises and Common dolphins are the most abundant species in the Celtic Sea with a density of 0.403 and 0.1 (animals/km^{-2}) respectively, while white-beaked and white-side dolphins are less abundant (0.0041 animals/km^{-2}) (Hammond et al., 2006).

The average weight for each species was calculated from the 'Poseidon' database (2005). The resulting biomass for 'toothed whales' was estimated to be 0.0397 (t km^{-2}). We calculated a weighted Q/B y^{-1} value of 18.594 from Sigurjonsson and Vikingsson (1997). A P/B y^{-1} value of 0.02 was given by Trites et al. (1999). Locally relevant diet composition data was available for 26 common dolphins (*Delphinus delphis*), based on examination of stranded individuals from the Normandy coast according to De Pierrepont et al. (2005). This diet was modified for input into Ecopath and based on: juvenile whiting 32%, mackerel 30%, horse mackerel 29%, trisopterus spp. 7%, pelagic fish 1%, and small benthic fish 1%.

3. Seals

The 'seal' group consists of grey seals *Halichoerus grypus* (F.) and harbor seals *Phoca vitulina* (L.). The grey seal population in the Celtic Sea was estimated to be 7552 individuals, based on 576 recorded in southwestern Ireland and 6976 individuals in south-west Wales (Kiely et al., 2000). The average body weight was assumed to be 134 kg (Bonner, 1994), and consequently the biomass was estimated to be 0.0045 (t km^{-2}) using equation 1.

The harbor seal population in the Celtic Sea was based on survey data from colonies in southern Ireland (937 individuals) (Cronin et al., 2003), together with an additional 20 animals in England & Wales (SCOS 2006). With an average body weight of 63.5 kg (Bonner, 1994), this yielded a biomass estimate for harbor seals of 0.0003 (t km^{-2}). Thus the total biomass of grey seals and harbor seals in the Celtic Sea was 0.0048 (t km^{-2}). Using the Trites et al. (1999) method, we calculated a Q/B y^{-1} value of 15.857 and a P/B y^{-1} value of 0.06.

As seal biomass was overwhelmingly dominated by grey seals, diet data for grey seals was used in the model. The diet of grey seals is modified from Kiely et al. (2000) and

based on: juvenile plaice 38%, 14% trisopterus spp. 14%, juvenile whiting 11%, small benthic fish 10%, squid 5%, pollack and saithe 4%, small pelagic fish 3%, juvenile cod 3%, juvenile hake 3%, horse mackerel 2%, small medium flatfish 2%, demersal predators 2%, sole 1% and juvenile blue whiting 1%.

Seabirds

The seabird group constitutes 15 species divided into 6 functional groups. Some groups were created on the basis of ecological similarity (diet and feeding habits) (i.e. seabird offshore-divers) (JNCC, 2008), however two species were kept as individual groups (Manx shearwater *Puffinus puffinus* and European storm petrel *Hydrobates pelagicus* (L.)). The biomass for each group represents the total population (breeders and non-breeders) for the colonies in the Celtic Sea region. Breeder counts were collated from the database Seabird 2000, and the number of non-breeders was calculated according to equations 2, 3, and 4:

Breeders number x productivity = number of chicks (y^{-1})

Equation 2

Number of chicks x juvenile survival rate (y^{-1}) = number of chicks after the first year

Equation 3

Number of chicks after 1 year x adult survival rate (y^{-1}) = number of non-breeders

Equation 4

Information on survival probability, productivity, and age at first breeding relative to each species are shown in Table 1. For those species where there was no published information about productivity and/or adult survival probability rate in the Celtic Sea (i.e. Northern fulmar *Fulmarus glacialis* (L.), European shag *Phalacrocorax aristotelis* (L.), Great cormorant *Phalacrocorax carbo* (L.), Lesser black-backed gull *Larus fuscus* (L.), Black headed gull *Larus ridibundus* (L.), and Herring gull *Larus argentatus* (L.), we used an average of the values relative to other species for the adults, and half values

for juveniles. For other species i.e. Black guillemot *Cepphus grille* (L.) information on the most similar species i.e. Common guillemot *Uria aalge* (P.) was used.

The seabird biomass in the area for each species was calculated by multiplying the abundance (breeders and non-breeders) by their body weight (equation 1), where the body weight for bird was calculated as an average between male and female (Table 2) (Snow and Perrins, 1998). The total biomass of each functional group was calculated successively as the sum of single species biomasses.

The total mortality rate (Z) of seabird was calculated as Z= fishing + natural mortality. Information was collected from published literature. However, this was possible only for few species as data on seabird bycatch in the Celtic Sea is very scarce. In the other cases the mortality rate was based only on natural mortality. A weighted P/B y^{-1} was calculated from adult survivor rate for the year and fishing mortality rate, available from literature sources (Table A3.1)

For each species food consumption for the year was calculated according to a bioenergetic model (Lauria and Votier, unpublished data) which estimated the energetic requirements of breeding and non-breeding adults, similarly to Votier et al. (2004b), based on the allometric equation of Ellis and Gabrielsen (2002), with a food assimilation efficiency of 0·75 (Hilton et al., 2000). These values were then weighted on the species biomasses to calculate a Q/B y^{-1} for each functional group.

Diet information was taken from the literature and adapted in Ecopath. In order to represent seabird migrations outside the Celtic Sea area part of the seabird diet was assumed as "import". These values were calculated by multiplying the original proportion of each prey item by the residence time ratio (days in the area/365). Information on length of time that each species spent in the area was taken from the Stanford and Pitcher (2004) model for the English Channel.

Table A3.1 Life table for seabird species in the Ecopath model.

Species	Adult survival probability average	Productivity	Juvenile survival	Age at first breeding	Fishing mortality	Sources
Northern gannet	0.77 (2 year) 0.79 (3 year) 0.81 (4 year) 0.82 (5 year)	0.75	0.26 (1 year)	4	0.005	Nelson, 2002; BirdLife International, 2009.
Black legged kittiwake	(1978-2007) 0.846	0.665 (1986-2007)	0.4 (1 year) 0.68 (2 year)	5	0.114	Chris Perrins (unpublished data relative to Skomer); Frederiksen et al., 2004; Snow and Perrins, 1998. BirdLife International, 2009.
Northern fulmar	0.86	0.66	0.37	6	2.076	Snow and Perrins, 1998. BirdLife International, 2009.
Common guillemot	(1986-2003) 0.945	0.79 (1973-2008)	0.69	6	NA	Votier et al., 2005; Chris Perrins (unpublished data relative to Skomer); Votier et al., 2008; Votier, unpublished data.
Atlantic puffin	(1973-2007) 0.907	0.665 (1986-2007)	0.88	5	NA	Chris Perrins (unpublished data relative to Skomer); Harris and Wanless, 1991; Snow and Perrins, 1998.
Razorbill	(1970-2007) 0.895	0.53 (1986-2007)	0.63	4	NA	Chapledaine, 1997; Chris Perrins (unpublished data relative to Skomer); Lavers et al., 2008.
Black guillemot	(1986-2003) 0.945	0.665	0.48	6	NA	Votier et al., 2005; Chris Perrins (unpublished data relative to Skomer); Votier et al., 2008; Votier, unpublished data.
Shag	0.86	0.66	0.51	3	NA	Potts et al., 1980; Snow and Perrins, 1998.
Great cormorant	0.86	0.66	0.58	3	NA	Frederiksen and Bregnballe, 2000; Snow and Perrins, 1998.
Lesser black-backed gull	(1978-2007) 0.88	0.66	0.44	4	NA	Chris Perrins (unpublished data relative to Skomer).
Herring gull	0.829	0.66	0.44	4	NA	Chris Perrins (unpublished data relative to Skomer).
Black-headed gull	(1978-2007) 0.88	0.66	0.44	4	NA	Snow and Perrins, 1998.
Manx shearwater	(1977-2007) 0.858	0.53	0.25	5	NA	Brooke, 1990; Snow and Perrins, 1998; Chris Perrins unpublished data.
European storm petrel	0.73	0.33	0.37	5	NA	Votier et al., 2006; Snow and Perrins, 1998.

Table A3.2 Information of abundance, biomass, and residence time of seabird species in the Celtic Sea area.

Species	Breeders and non-breeders abundance	Average weight per bird (t)	Total biomass (t)	Days in area
Northern gannet	66303	0.003	198.90	180
Black-legged kittiwake	36176	0.0004075	14.74	180
Northern fulmar	17311	0.00080625	13.95	365
Common guillemot	147076	0.0008615	126.70	240
Atlantic puffin	35058	0.0004	14.02	240
Razorbill	21991	0.000707	15.54	240
Black guillemot	1266	0.00042	0.53	240
Shag	7058	0.001957	13.81	365
Great cormorant	4119	0.0023	9.47	365
Lesser black-backed gull	67027	0.00075	50.26	180
Herring gull	4907	0.0008825	4.33	180
Great black-backed gull	41953	0.00167	70.06	365
Black-headed gull	2942	0.0002875	0.84	180
Manx shearwater	389928	0.000419	163.37	240
European storm petrel	10011	0.0000265	0.26	180

4. Seabird offshore-surface feeders

The offshore surface feeders group is composed of 3 species: Northern gannet *Morus bassanus*, Black-legged kittiwake *Rissa tridactyla*, and Northern fulmar *Fulmarus glacialis*. Biomass was calculated to be 0.0010 (t km^{-2}) in the Celtic Sea using equation 1. A weighted P/B y^{-1} (natural + fishing mortality) for the group was estimated to be 0.374. An empirical Q/B y^{-1} was calculated to be 98.78. A weighted diet for the group was based mainly on the assumption of: discards 14%, sole 13%, garfish 13%, pelagic fish 6% and small crustaceans (Votier et al., 2009 (unpublished data), Lewis et al., 2001, and Thompson et al., 1995).

5. Seabird inshore-divers

The inshore divers group is composed of three species: Great cormorant *Phalacrocorax carbo*, European shag *Phalacrocorax aristotelis* and Black guillemot *Cepphus grille*. Biomass was calculated to be 0.00010 (t km^{-2}) using equation 1. A weighted P/B y^{-1} (natural mortality only) for the group was estimated to be 0.138. Q/B y^{-1} was calculated to be 106. Diet information was taken from the literature and adapted for Ecopath. A weighted diet was mainly based on: pelagic fish 42%, small benthic fish 36%, pollack and saithe 11%, and fish juveniles (Liliendandahl and Solmundsson, 2007; Birkead et al., 2007).

6. Seabird offshore-divers

Three species constitute this offshore divers group: Common guillemot *Uria aalge*, Atlantic puffin *Fratercula artica*, and Razorbill *Alca torda*. Biomass was estimated to be 0.0007 (t km^{-2}) using equation 1. Weighted P/B y^{-1} (natural mortality only) and Q/B y^{-1} were calculated to be respectively 0.062 and 94.18. A weighted diet for offshore divers was modified from the literature (Birkead et al., 2007; Corkhill 1973; Liliendandahl and Solmundsson, 1997) and based mainly on pelagic fish (64%).

7. Gulls

The gull group is composed of: Lesser black-backed gull *Larus fuscus*, Herring gull *Larus argentatus*, and Black-headed gull *Larus ridibundus*. The total biomass was estimated to be 0.0006 (t km^{-2}) using equation 1. A weighted P/B y^{-1} (natural mortality only) for the group was calculated to be 0.119, while Q/B y^{-1} was estimated to be 130.15. Diet composition was assumed to be mainly: discards 51%, seabird offshore divers 8%, small crabs and other decapods 7%, bivalves 4%, and small crustaceans 4% (Buckley, 1990; Kubetzki and Garthe, 2003).

8. Manx shearwater

Manx shearwater *Puffinus puffinus* is the most abundant species in the Celtic sea, the biomass was calculated to be 0.00073 (t km^{-2}) using equation 1. P/B y^{-1} (natural mortality only) was estimated to be 0.141 and Q/B y^{-1} was calculated to be 205.610. Diet composition was adapted for Ecopath from Thompson (1987) and based on: squid 32%, pelagic fish 31%, and small crabs and other decapods 3%.

9. European storm petrel

European storm petrel *Hydrobates pelagicus* biomass was estimated to be 0.000001 (t km^{-2}) in the Celtic Sea area using equation 1. P/B y^{-1} (natural mortality only) was calculated to be 0.27 and Q/B y^{-1} was estimated in Ecopath. Diet composition was based mainly on: small crustaceans 19.7%, trisopterus spp. 9.27%, zooplankton 3.2%, and euphausiids 1.49% (D`Elbee and Hemery, 1998).

Fish Groups

For the Celtic Sea model we collected information on 62 different fish species, and combined these species into 34 functional groups (including multi-stanza groups) on the basis of feeding preferences or taxonomic similarity. For the commercially important species such as cod *Gadhus morhua*, blue whiting *Micromesistius poutassou* (R.), hake *Merluccius merluccius* (L.), plaice *Pleuronectes platessa* (L.), megrim *Lepidorhombus whiffiagonis* (W.), whiting *Merlangius merlangus* (L.), monkfish *Lophius* spp. and haddock *Melanogrammus aeglefinus* (L.) multi-stanza groups were implemented in Ecopath. The multi-stanza feature allows users to represent multiple ontogenic stages, biomass for juveniles (non-leading stanzas) are calculated using the von Bertalanffy prediction of relative body weight at age, which gives the relative biomass of each stanza.

Fish biomass estimates were calculated according this equation:

Biomass (t km^{-2}) = total catch biomass x catchability (q)

Equation 5

Estimates of biomass were taken from Cefas survey data (Tidd and Warnes, 2006) and they were averaged over the period of 1989-1993. A catchability value of 16% was assumed for all species based on Fraser et al. (2007). For small benthic species (i.e. dragonets, gobies, imperial scaldfish, thickback sole, three bearded rockling and scaldfish) data from a 2mbeam trawl survey of the Celtic Sea were used, where we assumed a catchability of 5-35% based on Ellis et al. (2002).

Under some assumptions the annual production rate (P/B) equals the total mortality rate (Z) and Z = M+F, where M is natural mortality and F is fishing mortality (Allen, 1971).

$$(P/B) = Z$$

Equation 6

$$Z = M+F$$

Equation 7

ICES landings statistics (available from www.ices.dk) were used for estimating the fishing mortality:

F= Landing + discards / Biomass

Equation 8

These were calculated as an average relative to the period 1989-1993 in the Celtic Sea divisions. Unfortunately it was not possible to add discard rate because there are no data available for this area, and this possibly reflects an underestimate of fishing mortality in the model. Natural annual mortality (M) was estimated for each species from the empirical model of Pauly (1980):

$$\text{Log}_{10} M = -0.2107 - 0.0824 \log_{10} W_{\infty} + 0.6757 \log_{10} k + 0.4687 \log_{10} T$$

Equation 9

Where k is the curvature parameter of the Von Bertalanffy growth function and T is the mean environmental temperature in ºC. A mean annual temperature of 12.77 ºC was used for the Celtic Sea based on COADS data for the region.

Consumption/biomass (Q/B) ratios were calculated according to the empirical model of Pauly et al. (1990) and Christensen and Pauly (1992):

$$Q/B = 10^{6.37} * 0.0313^{Tk} * W_{\infty}^{-0.168} * 1.38^{Pf} * 1.89^{Hd}$$

Equation 10

Where W_{∞} is the asymptotic weight of the fish; the most sensitive parameter, *Tk*, is the mean annual temperature expressed as 1000 / (T ºC + 273.1); *Pf* is a dummy variable expressing the feeding type and it is (1 for carnivorous such as apex predators, pelagic predators and zooplankton feeders and 0 for herbivorous and detritivorous). *Hd* characterizes the food type and is set at 1 for herbivores and 0 for carnivores. Generally, W_{∞} was calculated from L_{∞} using published values for the length/weight parameters *a* and *b*.

10., 11. Adult and juvenile Cod

Cod *Gadus morhua* is one of the most important top predators in the Celtic Sea ecosystem, although this species has been heavily depleted in recent years (Pinnegar et al., 2002). Adult cod biomass (age 2+) was estimated to be 0.425 (t km^{-2}) from the Cefas ground fish survey data for the Celtic Sea using equation 5, while juvenile biomass was calculated in Ecopath.

Natural mortality (M) was calculated to be 0.6810 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.117 for the spawning stock using equation 8; although juvenile F was calculated to be 0.1914 using an average of F values below the age of sexual maturity from ICES (2006a). P/B y^{-1} was calculated to be 0.798 for adults and 0.872 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 3.404 using equation 10, and for juveniles it was calculated in Ecopath and estimated to be 8.513. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult diet was primarily composed

of trisopterus 32%, and small benthic fish 22%. Juvenile diet was based mainly on small crabs and other decapods 49%, but also on trisopterus 25%.

12., 13. Adult and juvenile Blue whiting

Blue whiting *Micromesistius poutassou* is a major prey item for many other species and was split into two groups: adults (age 3+) and juveniles. Adult biomass was calculated to be 0.443 (t km^{-2}) using equation 5 (Cefas ground fish survey data). Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.696 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.003 for the spawning stock using equation 8. For juveniles, F was calculated to be 0.089 using an average of F values below the age of sexual maturity from ICES (2006). P/B y^{-1} for adult was calculated to be 0.699 and 0.785 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 6.666 using equation 10, and for juveniles was calculated in Ecopath to be 18.029. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult diet was composed of euphausiids 69% and pelagic fish 15%, while juvenile diet was composed almost exclusively of euphausiids 89%.

14., 15. Adult and juvenile Hake

Hake *Merluccius merluccius* is one of the most exploited species in the Celtic Sea (Pinnegar et al., 2002). The total adult biomass (age 4+) estimated for this region was 0.26 (t km^{-2}) using equation 5 (Celtic Sea ground fish survey data). Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.743 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.16 for the spawning stock using equation 8.

For juveniles, F was calculated to be 0.151 using an average of the F values below the age of sexual maturity from ICES (2005). P/B y^{-1} was calculated to be 0.903 for adults and 0.895 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 3.528 using equation 10. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult hake feed mainly on fish such as blue whiting 25%, mackerel 20%, and horse mackerel 20%, while the juvenile diet is based principally on blue whiting 56%, and trisopterus spp. 16%.

16., 17. Adult and juvenile Plaice

Plaice *Pleuronectes platessa* were split into 2 groups: adults (age 3+) and juveniles. Adult biomass was calculated to be 0.039 (t km^{-2}) using equation 5. Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.743 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.284 for the spawning stock using equation 8. For juveniles F was calculated to be 0.090 using an average of F values below the age of sexual maturity from ICES (2006a). P/B y^{-1} was calculated to be 1.027 for adults and 0.833 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 5.131 using equation 10 for the adults, and for juveniles was calculated in Ecopath to be 13.707. Adult diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult plaice diet consists mainly of polychaetes 76% and euphausiids 21%. Juvenile plaice were assumed to consume mainly zooplankton groups.

18., 19. Adult and juvenile Megrim

Megrim *Lepidorhombus whiffiagonis* is one of the most important commercial species in the Celtic Sea (Pinnegar et al., 2002). Adult biomass (age 2+) was estimated for this region to be 0.194 (t km^{-2}) (Celtic Sea ground fish survey data) using equation 5. Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.765 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.18 for the spawning stock using equation 8. For juveniles, F was calculated to be 0.024 using an average of F values below the age of sexual maturity from ICES (2005). P/B y^{-1} was calculated to be 0.945 for adults and 0.789 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 3.819 using equation 10 for the adults, and for juveniles was calculated in Ecopath to be 7.777. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al. 2003). Adult megrim feed mainly on fish such as trisopterus spp. 40%, blue whiting 20%, and horse mackerel 14%, while juveniles consume blue whiting 14% and small crustaceans such as euphausiids 21%, small crabs and other decapods 27%.

20., 21. Adult and juvenile Whiting

The biomass of adult whiting *Merlangius merlangus* (age 2+) was estimate to be 0.412 (t km^{-2}) from Celtic Sea ground fish survey data using equation 5. Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.922 across all age groups using equation 9. Fishing mortality (F) was calculated to be 0.133 for the spawning stock using equation 8. For the juveniles F was calculated to be 0.025 using an average of F values below the

age of sexual maturity from ICES (2006). P/B y^{-1} was calculated to be 1.055 for adults and 0.804 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 3.874 using equation 10, and for juvenile was calculated in Ecopath to be 8.798. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult whiting diet was dominated by fish i.e. trisopterus spp. 39% and pelagic fish 21%. Juvenile whiting feed mainly on pelagic fish 44%, and euphausiids 18%.

22., 23. Adult and juvenile Monkfish

Monkfish are the anglerfish *Lophius piscatorius* (L.) and white bellied anglerfish *Lophius budegassa* (S.). Adult monkfish biomass (age 6+) was calculated to be 0.290 (t km^{-2}) from Celtic Sea ground fish survey data using equation 5. Juvenile biomass was calculated in Ecopath.

Natural and fishing mortality were estimated using equations 9 and 8, and were estimated to be 0.841 and 0.198 for the adults. Juvenile fishing mortality was calculated to be 0.242 using an average of fishing mortality values below the age of sexual maturity from ICES (2005). P/B y^{-1} was calculated to be 1.039 for adults and 1.084 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 2.555 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that adult monkfish feed mainly on mackerel 46% and horse mackerel 15%, small and medium flatfish 10%; while juvenile diet is dominated by small and medium sized flatfish 38%, small benthic fish 24% and trisopterus spp. 18%.

24., 25. Adult and juvenile Haddock

Haddock *Melanogrammus aeglefinus* were split into 2 components: adult (age 2+) and juvenile. Adult biomass was calculated to be 0.159 (t km^{-2}) from Cefas ground fish survey data using equation 5. Juvenile biomass was calculated in Ecopath.

Natural mortality (M) was estimated to be 0.727 across all age groups using equation 9. Fishing mortality (F) was estimated to be 0.053 for the spawning stock using equation 8. For juveniles F was calculated to be 0.210 using an average of F values below the age of sexual maturity from ICES (2006a). P/B y^{-1} was calculated to be 0.78 for adults and 0.938 for juveniles using equations 6 and 7.

Q/B y^{-1} was calculated to be 4.657 using equation 10. Diet information was taken from the Cefas fish stomach contents database (Pinnegar et al., 2003). Adult haddock diet was assumed to be composed largely of fish (trisopterus spp. 24%, mackerel 20%, horse mackerel 18%, and pelagic fish 14%), while juvenile diet was based on benthic invertebrates (Echinoderms 52%), in particular ophiuroids, bivalves 14% and small crabs and other decapods 17%.

26. Sole

Sole *Solea solea* (L.) biomass was estimated to be 0.053 (t km^{-2}) from Celtic Sea ground fish survey data. P/B y^{-1} was calculated based on M and F values, which were estimated at 0.719 and 0.097 respectively, using equations 8 and 9 and estimated to be 0.811. Q/B y^{-1} was estimated to be 5.722 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that adult Sole feed predominantly on epifaunal mesobenthos (polychaetes 61%, echinoderms 39%).

27. Mackerel

Mackerel *Scomber scombrus* are a highly migratory species that use the Celtic Sea primarily as a nursery ground. The original biomass value was calculated in Ecopath because it was thought that the original value from the ground fish survey might be affected by the fact that the survey is designed specifically to catch this species, as it appeared inflated; also the ICES stock assessment for this species relates to the North-east Atlantic and information is limited for the Celtic Sea.

P/B y^{-1} was estimated to be 0.6451 while Q/B y^{-1} was estimated to be 1.73 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that mackerel feed primarily on: euphausiids 39%, zooplankton 37 %; small crabs and other decapods 9%, horse mackerel 6%, plankton 2%, pelagic fish 2%, and some instances of cannibalism 1%.

28. Horse mackerel

Horse mackerel *Trachurus trachurus* is another highly migratory species that over winter in the Celtic sea but migrate northward along the shelf edge between July and September (returning southward between September and December). Smaller, younger fish do not travel as far and immature fish stay in the Celtic sea area, with some movement into the English Channel (Eaton, 1983). Biomass value was calculated in Ecopath because it was thought that the original value from the ground fish survey might be affected by the fact that the survey is designed specifically to catch this species as it appeared inflated; also the ICES stock assessment for this species relates to the North-east Atlantic and information is limited for the Celtic Sea.

P/B y^{-1} was estimated to be 0.688 using equations 6 and 7. Q/B y^{-1} was calculated to be 3.51 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that Horse mackerel feed mainly on: euphausiids 74% and zooplankton

(copepods) 24%, and to a lesser extent upon gastropods 1% and small crabs and other decapods 1%.

29. Red mullet

Red mullet *Mullus surmuletus* (L.) biomass was calculated from ground fish survey data for the Celtic Sea and was estimated to be 0.069 (t km^{-2}). Natural and fishing mortality were calculated using equations 9 and 8 and were estimated to be 0.730 and 0.005 respectively. P/B y^{-1} was calculated to be 0.735 using the equations 6 and 7. Q/B y^{-1} was calculated to be 5.962 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that red mullet feed primarily on: polychaetes 39%, small crabs and other decapods 27%, echinoderms 24%, large crabs and lobster 8%, and small crustaceans 2%.

30. Sea bass

Sea bass *Dicentrarchus labrax* (L.) biomass was calculated to be 0.408 (t km^{-2}) for the Celtic Sea from data collected through a fishery and biological sampling program around England and Wales (Pawson et al., 2007).

Natural and fishing mortality were estimated to be 0.778 and 0.008 respectively using equations 9 and 8. P/B y^{-1} was calculated to be 0.786. Q/B y^{-1} was estimated to be 4.407 using equation 10. The sea bass diet is modified from Pickett and Pawson (1994) and comprises: mackerel 40%, small crabs and other decapods 40%, small pelagic fish 9%, pelagic fish 6%, squid 3%, trisopterus spp. 2%, small benthic fish 1% and polychaetes 1%.

31. Large sharks

Large sharks include tope *Galeorhinus galeus* (L.) 99%, porbeagle *Lamna nasus* (B.) and blue sharks *Prionace glauca* (L.) (<1%). Total biomass was calculated from Cefas survey data and was estimated to be 0.646 (t km^{-2}).

Natural and fishing mortality were estimated using equations 9 and 8, and therefore we calculated a weighted P/B y^{-1} value of 0.819. Q/B y^{-1} was calculated to be 3.452 using equation 10 and weighted for the group. A weighted diet was calculated and adjusted in the model for the group (Henderson et al., 2000; Joyce et al., 2002; Stanford and Pitcher, 2004) and was based on: whiting 33%, pelagic fish 33%, small and medium flatfish 17%, and mackerel 17%.

32. Small sharks

Small sharks include spurdog *Squalus acanthias* (L.) and starry smooth hound *Mustelus asterias* (C.). Biomass data was calculated from Cefas survey data and was estimated to be 1.521 (t km^{-2}).

Natural and fishing mortality were estimated using equations 9 and 8, and therefore we calculated a weighted P/B y^{-1} value of 0.113 using equations 6 and 7. Q/B y^{-1}, weighted for the group, was estimated to be 4.739 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that this group feed mainly on mackerel 34%, and small crabs and other decapods 15%.

33. Pelagic fish

The Pelagic fish group is composed of pilchard *Sardina pilchardus* 45%, herring *Clupea harengus* 35%, sprat *Sprattus sprattus* 14%, and anchovy *Engraulis encrasicolus* (L.) 4%. Total biomass was estimated to be 0.046 (t km^{-2}) from ground fish survey data for the Celtic Sea. Natural and fishing mortality were estimated using equations 9 and 8, and then a weighted P/B y^{-1} was calculated to be 0.655 for the group. Q/B y^{-1} was estimated to be 7.915 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that pelagic fish feed mainly on: euphausiids 82%, gastropods 9%, cannibalism 4%, small pelagic fish 2%, zooplankton 2%, and small crustaceans 1%.

34. Ray & skates

Ray and skates include common skate *Raja batis* (L.) 31%, blonde ray *Raja brachyura* (G.) 22%, thornback ray *Raja clavata* (L.) 20%, cuckoo ray *Leucoraja naevus* (M.) 16%, and spotted ray *Raja montagui* (F.) 10%. Biomass data was calculated from Celtic Sea ground fish survey data and was estimated to be 0.879 (t km^{-2}). Natural and fishing mortality were estimated using equations 9 and 8, and therefore we calculated a weighted P/B y^{-1} value of 0.387 using equations 6 and 7. Q/B y^{-1}, weighted for the group, was estimated to be 3.798 and calculated using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that ray and skate diet is composed mainly of: small crabs and other decapods 84%, euphausiids 5%, horse mackerel 2%, and polychaetes 2%. Juvenile whiting, mackerel, small benthic fish, large crabs and lobster, cuttlefish, and squid account for the remaining 1%, or less. It is interesting to note that common skate were considerably more abundant in the catch in the 1990s compared to the present day (John Pinnegar personal comments).

35. Turbot and brill

Turbot and brill *Scophthalmus cynoglossus; S. rhombus* (L.) biomass were estimated from ground fish survey data to be 0.305 (t km^{-2}). Natural and fishing mortality were calculated using equations 9 and 8, and therefore using equations 6 and 7 a weighted P/B y^{-1} value was estimated to be 0.592. Q/B y^{-1}, weighted for the group, was calculated to be 5.324 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that the diet of these species is composed of: euphausiids 52%, small crabs and other decapods 33%, small benthic fish 7%, large crabs and lobster 4%, polychaetes 2%, and gastropods 1%.

36. Small and medium flatfish

Small and medium flatfish include thickback sole *Microchirus variegatus* (D.) 26%, lemon sole *Microstomus kitt* (W.) 24%, imperial scaldfish *Arnoglossus imperialis* (R.)

20%, dab *Limanda limanda* (L.) 18%, witch *Glyptocefalus cynoglossus* (L.) 10%, and scaldfish *Arnoglossus laterna* (W.) 2%. Biomass of scaldfish, thickback sole, and imperial scaldfish were based on 2mbeam trawl data, assuming a catchability of 35%, from Ellis et al. (2002). Biomass for the other species was estimated from ground fish survey data. The total biomass was calculated to be 0.508 (t km^{-2}) (Tidd and Warnes, 2006).

Natural and fishing mortality were calculated using equations 9 and 8, and therefore a weighted P/B y^{-1} value was estimated to be 0.683 using equations 6 and 7. Q/B y^{-1}, weighted for the group, was calculated to be 7.767 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that these species feed on: polychaetes 40%, sessile invertebrates 15%, small crabs and other decapods 14%, bivalves 12%, euphausiids 10%, large crabs and lobster 6%, echinoderms 2% and small benthic fish 2%.

37. Trisopterus spp.

The Trisopterus group is composed mainly of poor cod *Trisopterus minutus* (L.) 60% and bib *Trisopterus luscus* (L.) 22%, while norway pout *Trisopterus esmarki* (N.) and silvery pout *Gadiculus argenteus* (G.) account for less than 18%. Biomass was estimated to be 1.890 (t km^{-2}) from ground fish survey data in the Celtic sea.

Natural and fishing mortality were calculated using equations 9 and 8, and therefore a weighted P/B y^{-1} value was estimated to be 0.252 using equations 6 and 7. Weighted Q/B y^{-1} for the group was calculated to be 7.460 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that the diet of these species is composed of: small crabs and other decapods 42%, euphausiids 34%, small and medium flatfish 6%, polychaetes 5%, small benthic fish 3%, cuttlefish 3%, squid 3%, large crabs and lobster 2%, small crustaceans 1% and gastropods 1%.

38. Gurnards

The Gurnards group is composed of grey gurnards *Eutrigla gurnardus* (L.) 41%, red gurnard *Aspitrigla cuculus* (L.) 37% and tub gurnard *Trigla lucerna* (L.) 22%. Total biomass was estimated to be 0.406 (t km^{-2}) from ground fish survey data. Natural and fishing mortality were estimated using equations 9 and 8, therefore a weighted P/B y^{-1} was calculated to be 0.689 for the group using equations 6 and 7. Q/B y^{-1} was estimated to be 5.621 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that gurnards feed mainly on small crabs and other decapods 63%, and euphausiids 27%.

39. Pollack and saithe

Pollack *Pollachius pollachius* (L.) 63% and saithe *P. virensis* (L.) 37% biomass was calculated to be 3.818 (t km^{-2}) from ground fish survey data in the Celtic sea. Natural and fishing mortality were estimated using equations 9 and 8, therefore a weighted P/B y^{-1} was calculated to be 0.787 for the group using equations 6 and 7. Q/B y^{-1} was estimated to be 3.582 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that Pollack and saithe feed mainly on pelagic fish 33%, mackerel 28%, and trisopterus spp. 27%.

40. Small benthic fish

Small benthic fish include mainly dragonets (Callyonimidae) 73% and three bearded rocking *Gaidropsarus vulgaris* (C.) 14%, while gobies *Pomatochistus* spp., lesser weever *Trachinus vipera* (C.), and pogge *Agonus cataphractus* (L.) represent the smaller component of 13%. Biomass data were estimated to be 0.129 (t km^{-2}) from Ellis et al. (2002) and the Celtic sea ground fish survey. Natural and fishing mortality were estimated using equations 9 and 8, therefore a weighted P/B y^{-1} was calculated to be 0.475 for the group. Q/B y^{-1} was estimated to be 8.681 using equation 10. The Cefas

fish stomach contents database (Pinnegar et al., 2003) indicates that their diet is composed mainly of polychaetes 36%, nematodes 36%.

41. Small pelagic fish spp.

Small pelagic fish spp. includes mainly boarfish *Capros aper* (L.) 97%, whereas lesser silver smelt *Argentina spyraena* (L.), snipe fish *Macrorhomphosus scolopax* (L.) and pearlside *Maurolicus muelleri* (G.) account for less than 3%. Biomass was calculated to be 2.550 (t km^{-2}) from the Celtic Sea ground fish survey. Natural and fishing mortality were estimated using equations 9 and 8, therefore a weighted P/B y^{-1} was calculated to be 0.655 for the group. Q/B y^{-1} was estimated to be 9.245 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that diet is composed of: zooplankton (copepods) 90%, euphausiids 6%, carnivorous macroplankton 3%, and small crustaceans 2%.

42. Garfish

Garfish *Belone belone* is a pelagic fish that lives close to the surface and has a migratory pattern similar to mackerel. This fish is an important component of the seabird diet, especially Northern gannets. Unfortunately no data were available to estimate its biomass in the Celtic Sea, therefore biomass was calculated in Ecopath by using and Ecotrophic Efficiency (EE) value of 0.95. P/B y^{-1} was calculated to be 0.676 using equations 6 and 7, and Q/B $y^{-1}$was estimated to be 4.87 using equation 10. The diet of garfish is modified from Dorman (1991) and assumed to be based on: pelagic fish 51%, gastropods 21%, polychaetes 19%, small crustaceans 8%, and bivalves 1%.

43. Demersal predators

The demersal predator group is composed of: conger eel *Conger conger* (L.) 52%, john dory *Zeus faber* (L.) 37%, greater forkebeard *Phycis blennoides* (B.) 7% and blue-mouth redfish *Helicolenus dactylopterus* (D.) 3%. Total biomass was estimated to be

0.570 (t km^{-2}) from ground fish survey data. Natural and fishing mortality were estimated using equations 9 and 8, therefore a weighted P/B y^{-1} was calculated to be 0.779 for the group using equations 6 and 7. Q/B y^{-1} was estimated to be 3.938 using equation 10. The Cefas fish stomach contents database (Pinnegar et al., 2003) indicates that diet is composed of: horse mackerel 29%, mackerel 22%, pelagic fish 16%, trisopterus spp. 9%, large crabs and lobster 6%, small crabs and other decapods 4%, juvenile whiting 4%, small and medium flatfish 2%, small benthic fish 2%, blue whiting 1%, juvenile blue whiting 1%, gurnards 1% and cuttlefish 1%.

Invertebrate groups

Cefas 2m Beam trawl survey data were used to estimate invertebrate epifaunal biomass, using equation 3 with a catchability range value of 5-35% (Kaiser et al., 1994). To evaluate the invertebrate infaunal biomass data from CEFISB 06 for the Irish Sea were used. For other groups (small crabs and other decapods, small crustacea, bivalves, gastropods, echinoderms and polychaetes) epifaunal and infaunal biomasses were added together.

The biomass of the main commercial invertebrate groups (edibile grabs, lobster, scallops and cuttlefish) in the Celtic Sea was estimated from the SW COBAS 1991 survey. Zooplankton (copepods and cladocerans) biomass estimates were calculated from the continuous plankton recorder (CPR) database. For the other invertebrate groups biomass information was taken from the published literature for the area (Joint and Williams, 1985; Vanaverbeke et al., 1997; van Duyl et al., 1993; Poremba and Hoppe, 1995).

There was only limited quantitative information in the literature on invertebrate diet, therefore where possible we used this information, otherwise it was taken from published Ecopath models covering the English channel (Stanford and Pitcher 2004,

Araujo et al., 2005), Irish sea (Lees and Mackinson, 2007) and North Sea (Mackinson and Daskalov 2007).

For invertebrate species F and Z estimates were rarely available. To calculate P/B y^{-1} ratios for these groups Brey`s (2002) multi parameter P/B y^{-1} model (version 4.04) was used to estimate the annual somatic production-to-biomass ratio of benthic invertebrate populations.

Mean weight for each species was calculated from Cefas 2mBeam trawl survey data (Ellis et al., 2002) and a weighted average was calculated where groups contained more than one species. In some cases mean wet weight was converted to mean shell-free wet weight for the purpose of calculating P/B values. After first converting to shell free weights, wet weight was converted to kilo joules using Brey conversion J/mgWM.

Where possible, species specific conversions were obtained from Brey conversions database, otherwise the mean conversion factors were obtained from values reported for species within the same taxonomic family, order, subclass, or class, whichever was the lowest resolution, with the number of records greater than 10 (under advice of T. Brey). For other groups P/B y^{-1} was estimated from the literature. In the absence of other data to calculate Q/B y^{-1} we used published food conversion efficiency values P/Q y^{-1} from other models, as shown in Table A3.3:

Table A3.3 Food conversion efficiency values P/Q year $^{-1}$ for invertebrate groups.

Groups	**P/Q y $^{-1}$**	**Source**
Small crabs and other decapods	0.15	Christensen, 1995
Large crabs and lobsters	0.15	Christensen, 1995
Small crustaceans	0.15	Christensen, 1995
Bivalves	0.09	Stanford and Pitcher, 2004
Gastropods	0.15	Christensen, 1995
Cuttlefish	0.15	Pauly and Christensen, 1995
Sessile invertebrates	0.25	Haggan and Pitcher, 2005 (based on Morrisette et al., 2003).
Echinoderms	0.25	Haggan and Pitcher, 2005 (based on Morrisette et al., 2003).
Polychaetes	0.15	Stanford and Pitcher, 2004
Nematodes	0.15	Mackinson and Daskalov, 2007

44. Small crabs and other decapods

Small crabs and other decapods is composed of anomuras 58% (i.e. *Munida rugosa* (F.), *Pagurus prideauxi* (L.), *Pagurus bernhardus* (L.)), small crabs 21% (i.e. *Macropipus tuberculatus* (R.); and *Liocarcinus spp.*), shrimps and prawns 17% (i.e. *Processa canaliculata* (L.); *Dichelopandalus bonneri* (C.); *Crangon* allmanni (K.)) and Norway lobster 4% *Nephrops norvegicus* (L.). Biomass data was calculated from Celtic Sea 2m beam survey data and was estimated to be 0.879 (t km^{-2}).

A weighted P/B y^{-1} value was calculated to be 0.95 using T. Brey model (2002). Q/B y^{-1} was estimated to be 6.332 using a gross food conversion efficiency value of 0.15. The diet of small crabs and other decapods is modified from Stanford and Pitcher (2004) and assumed to be 62% detritus, 20% bivalves, and 18% cannibalism.

45. Large crabs and lobster

The large crabs and lobster group comprises edible crabs 98% and lobster 2%. Biomass was calculated to be 0.393 (t km^{-2}) from Cefas survey data (SW COBAS project). A weighted P/B y^{-1} value was estimated to be 0.381 using T. Brey model (2002). Q/B y^{-1} was calculated to be 2.54 using a gross food conversion efficiency value of 0.15. According to Stanford and Pitcher (2004) large crabs and lobster diet is composed of: small crabs and other decapods 18%, bivalves 20%, and detritus 62%.

46. Small crustaceans

Small crustaceans is composed for the most part of: small crabs 66%, barnacles 23% (i.e. *Scalpellum scalpellum* (L.)), isopods 8% for example *Eurydice pulchra* (L.), *Circolana cranchii* (L.) and amphipods 4% (*Ampelisca* spp.). Biomass was estimated to be 0.56 (t km^{-2}), from Celtic Sea 2m beam survey data. A weighted P/B y^{-1} value was estimated to be 3.456 using T. Brey model (2002). Q/B y^{-1} was calculated to be 23.039

using a gross food conversion efficiency value of 0.15. Small crustaceans diet was assumed to be entirely composed of detritus (Stanford and Pitcher, 2004).

47. Bivalves

Bivalve biomass was calculated to be 25.32 (t km^{-2}), from Celtic survey data and is composed for the most part of bivalves 52% for example *Nucula sulcata* (B.), *Aequipecten opercularis* (L.), and scallops 48% *Pecten maximus* (L.). A weighted P/B y^{-1} value was estimated to be 1.104 using T. Brey model (2002). Q/B y^{-1} was estimated to be 12.266 using a gross food conversion efficiency value of 0.09. We found little quantitative information on the diet of bivalves, but it is assumed to be a combination of phytoplankton and detritus; hence 50% of each of these components were included (Stanford and Pitcher, 2004).

48. Gastropods

Gastropod biomass data was calculated from Cefas survey data (SW COBAS project) and estimated to be 1.765 (t km^{-2}). This group is composed of 76% gastropods (mainly *Turritella communis* (R.), and *Aphorrais pespelecani* (L.), 16% mollusca, 7% opistobranchis *Scaphander lignarius* (L.), and 1% turkshells *Antalis entails* (L.). A weighted P/B y^{-1} value was estimated to be 0.655 using T. Brey model (2002). Q/B y^{-1} was calculated to be 4.36 using a gross food conversion efficiency value of 0.15. Diet composition was estimated from the literature and assumed to consist exclusively of detritus (Younge, 1946).

49. Cuttlefish

Cuttlefish biomass data was estimated to be 0.186 (t km^{-2}) from Cefas survey data (SW COBAS project). A weighted P/B y^{-1} value was estimated to be 0.212 using T. Brey model (2002). Q/B y^{-1} value was estimated to be 15 (Stanford and Pitcher, 2004; Mackinson and Daskalov, 2007). Cuttlefish diet is modified from Alves et al. (2006)

and assumed to be: pelagic fish 27%, small pelagic spp. 27%, cannibalism 6%, squid 6%, small crustaceans 9%, small crabs and other decapods 8%, small and medium flatfish 7%, bivalves 5%, and small benthic fish 4%.

50. Squid

Squid biomass was calculated in Ecopath by using an EE of 0.95. Therefore P/B y^{-1} and Q/B y^{-1} values were estimated to be respectively 3 and 15 (Okey and Pauly, 1999). Diet composition was taken from the literature (Pierce et al., 1994) and is assumed to be almost entirely euphausiids 97%.

51. Sessile invertebrates

Sessile invertebrates are composed mainly of Anthozoa *Caryophyllia smithii* (S.), *Actinauge richardi* (M.) 95%, and Hydroids, Sponges, Bryozoa and Tunicates account for 3%. Biomass was calculated from Cefas survey data (SW COBAS project) and was estimated to be 3.811 (t km^{-2}). A weighted P/B y^{-1} value was estimated to be 0.645 using T. Brey model (2002). Q/B y^{-1} value was calculated to be 2.58 using a P/Q value of 0.25. Diet composition is based on Stanford and Pitcher (2004) and assumed to be: zooplankton 45%, detritus 35%, phytoplankton 10%, and nematodes 10%.

52. Echinoderms

The Echinoderm group is composed of: asteroidea 53%, echinodea 27%, starfish and brittlestars 12%, urchins 7%, and holothurians 1%. Biomass was calculated from Cefas survey data (SW COBAS project) and estimated to be 7.459 (t km^{-2}). A weighted P/B y^{-1} value was estimated to be 1.376 using T. Brey model (2002). Q/B y^{-1} value was calculated to be 5.504 using a P/Q value of 0.25. According to Stanford and Pitcher (2004) diet is composed of: detritus 72%, polychaetes 11%, echinoderms 6%, phytoplankton 5%, bivalves 5%, and sessile invertebrates 1%.

53. Polychaetes

Polychaete biomass was estimated to be 20.815 (t km^{-2}) from Cefas survey data (SW COBAS project). The main species in this group are *Orbinia sertulata* (S.), *Euclymene lumbricoides* (Q.), and *Glycera rouxii* (A.). A weighted P/B y^{-1} value was estimated to be 1.963 using T. Brey model (2002), Q/B y^{-1} value was calculated to be 13.088 using a P/Q value of 0.15. Diet is assumed to be composed entirely of detritus (POM 40% DOM 30%), and benthic bacteria 30% (Christensen, 1995).

54. Nematodes

For the Celtic sea area there is no known information about biomass, P/B and Q/B. Nematode biomass was estimated to be 0.063 (t km^{-2}) from the literature (Vanaverbeke et al., 1997) using a correction factor of 22.5% from dry to wet weight (Kennedy, 1994). P/B y^{-1} was estimated to be 2.5 (from Stanford and Pitcher, 2004), while Q/B y^{-1} value was calculated to be 16.666 using a P/Q value of 0.15. Diet is taken from the Stanford and Pitcher model (2004) and based on 70% POM and 20% benthic bacteria.

55. Zooplankton

An average of biomass of zooplankton (copepods and cladocerans) was calculated from the Celtic CPR data (SAHFOS) and estimated to be 19.777 (t km^{-2}). From the original dataset densities were converted in biomass (mg m^{-3}) using appropriate correction factors using the equations 11 and 12:

Biomass (mg m^{-3}) = Average biomass (mg m^{-3}) * correction factor

Equation 11

Biomass (gr m^{-2}) = 1000* biomass (mg m^{-3}) * average depth (83.733 m)

Equation 12

P/B y^{-1} and Q/B y^{-1} were estimated to be respectively 18 and 60 (Stanford and Pitcher, 2004), while diet is based on: phytoplankton 90%, DOM 7% and zooplankton 3% (Stanford and Pitcher, 2004).

56. Carnivorous macroplankton

Carnivorous macroplankton is composed of chetognaths and jellyfish. The total biomass for the Celtic Sea was estimated from the literature to be 0.642 (t km^{-2}) (Conway and Williams, 1986; Weisse and Gomoiu, 2000) using a correction factor of 11.5 from dry weight to wet weight (Cauffope and Heymans, 2005). P/B y^{-1} and Q/B y^{-1} were estimated to be respectively 7 and 23.33 (Stanford and Pitcher, 2004). Diet is composed entirely of zooplankton (Stanford and Pitcher, 2004).

57. Euphausiids

According to Joint and Williams (1985) two main species of euphausiids occur in the Celtic sea, *Nyctiphanes couchi* (B.) and *Meganyctiphanes* norvegica (S.). For our model we estimated an average biomass of 9.684 (t km^{-2}). This value was calculated from an average biomass expressed as 950 (mgC m^{-2}) using different correction factors to convert carbon to grams of wet weight (Cauffope and Heymans, 2005). Zooplankton was sampled daily using the double Longhurst Hardy Plankton recorder (LHPR), fitted with 280 and 53 µm mesh nets.

There is not much information available about the ratio P/B in the Celtic Sea, for this reason we calculated this value in Ecopath. Joint and Williams (1985) estimate a food requirement of between 9 and 114 (mgC m^{-2} d^{-1}). According to Lasker (1966), we calculated a value of 23.631 for Q/B y^{-1} using an appropriate conversion factor to convert carbon to grams of wet weight (Cauffope and Heymans, 2005). Diet composition is assumed to be: zooplankton 23%, phytoplankton 57%, POM 18%, and carnivorous macroplankton 2% (Mackinson and Daskalov, 2007).

58. Microflagellates

Microflagellate counts include photosynthetic flagellates, which were the organisms responsible for primary production in the >5 to <1 µm size fraction (Joint and Pipe,

1984). We calculated a biomass of 2.720 (t km^{-2}) for the Celtic Sea region on the estimate of carbon that Joint and Williams (1985) calculated for the same area (29928 mgC m^{-2}), this value was successively corrected with a conversion factor (Cauffope and Heymans, 2005). P/B y^{-1} was estimated to be 200 and Q/B y^{-1} was calculated to be 400 using a P/Q of 0.5 (Christensen, 1995). According to Joint and William (1985) diet is composed entirely of pelagic bacteria.

59. Pelagic bacteria

Pelagic bacteria have recently been recognized as playing a very important part in the flow of carbon in the pelagic ecosystem (Williams, 1981). Biomass was calculated to be 0.875 (t km^{-2}), based on estimates of carbon that Joint and Williams (1985) calculated for the Celtic sea area (8754600 mg C m^{-2}), this value was converted using a conversion factor of 10% from carbon to wet weight (Mathews and Heimdal, 1980).

Joint et al. (2001) estimated bacterial production and consumption to be respectively 12 gr C m^{-2} y^{-1} and 28gr C m^{-2} y^{-1}. We calculated P/B y^{-1} and Q/B y^{-1} to be respectively 137.117 and 319.941 using the same conversion factor as above. Diet was assumed to be composed entirely of dissolved organic matter.

60. Benthic bacteria

Benthic bacteria are an important component of marine ecosystems, they are responsible for the utilization of the extensive pool of dissolved organic matter (DOM), thus making it available for the food web in this layer. In deep sea sediments bacteria account for about 90% of the total biomass (Pfannkuche, 1993).

In the Celtic Sea we calculated the biomass to be 3.247 (t km^{-2}), this value agree with Poremba and Hoppe (1995) who calculated a biomass of 3.247 micro gr C l^{-1} in the same area, this value was converted using an appropriate correction factor (Mathews and Heimdal, 1980). P/B y^{-1} was calculated to be 2.783 using an average of the bacterial

production in the area (Poremba and Hoppe, 1995). Q/B y^{-1} was estimated to be 247.283 according to Van Duyl et al. (1993). Diet is assumed to be composed of 100% DOM.

61. Phytoplankton

Phytoplankton biomass was calculated using data obtained from the OMEX I project where the biological production in the surface waters of the Celtic sea was measured. Data were provided by the Continuous Plankton Recorder (CPR) survey index of green color between 1963 and 1995. These data have the greatest sampling density and frequency for phytoplankton biomass in the Celtic sea area, and therefore provide the best description of the mean-decadal seasonal cycle of abundance. According to Joint et al. (2001) we calculated an average of 35.507 mg $chla^a m^{-2}$ that was converted using a conversion factor of 1 mg $chla^a$ = 1140 mg WW; 114,00mg/m^2 = 114g/m^2 (Strickland, 1960) to estimate a biomass value of 40.477 (t km^{-2}). The production was estimated to be 186 grC m^{-2} y^{-1} (Joint and Pomroy, 1987) and using a conversion factor of 1 grC = 9 grWW (Pauly and Christensen, 1995) we calculated a production of 1680.23 grams of WW, P/B y^{-1} was estimated to be 41.511.

62. Particulate Organic Matter

Joint and Williams (1985) estimated that the particulate organic carbon concentration in the Celtic Sea is about 100 gr C l^{-1} above the thermocline and 50 gr C l^{-1} below it. Considering that in this area the average depth is 83.7 m and the thermocline is about 30 m depth we calculated a total of 5.6850 gr C m^2. The final biomass was calculated to be 56.85 (t km^{-2}) using a conversion factor of 1 gr C = 10 gr WW (Arias-Gonzales, 1994).

63. Discarded fish

The total Celtic sea discards were divided by the area of the Celtic sea to give a discard biomass estimate of 1.39 (t km^{-2}).

64. Dissolved Organic Matter

The dissolved organic matter is estimated using an empirical relationship that relates detritus biomass to primary productivity. According to Cauffope and Heymans (2005) DOC=16% of total phytoplankton production. Using this conversion factor a DOC biomass value was estimated to be 268.83 (t km^{-2}) relative to the Celtic Sea.

Fisheries data

Landings data

International landings of fish and shellfish were obtained from ICES Fishstat plus (ICES area VII f-j) database and an average from 1989-93 was calculated for each country (UK, Ireland, France, Spain, Belgium, Denmark, Germany and Netherlands). Unfortunately these data are not broken down into gear types, and for this reason all fishery landings were allocated to two gear types or fleets. Catches of pelagic schooling species including Mackerel, horse mackerel, and clupeids were allocated to the pelagic fleet category. Landings of demersal fish including cod, hake, megrim, whiting, monkfish, haddock, red mullet, seabass, large sharks, turbot and brill, small and medium flatfish, trisopterus spp., and demersal predators were allocated to the demersal fleet. Commercially important crustacea, mollusca and cephalopods in the model (i.e. small crabs and other decapods, large crabs and lobster, bivalves, cuttlefish and squid) were also allocated to the demersal fleet. For each functional group landings were assigned and expresses as t/km^2.

Discard data

Discards or offal are defined as that portion of the total organic material of animal origin in the catch, which is thrown away or dumped at the sea (Kelleher, 2005). This is because fishing gears are generally not fully selective for the target species, and

therefore catches include certain species, size classes or damaged fish that have low market value. Discards data were not available for the Celtic Sea, however for some groups they were calculated by using the rate of retains and discards available in the literature (Perez et al., 1996; Rochet et al., 2002; Borges et al., 2005; Enever et al., 2007; John Casey personal comments). Discard values for France, Ireland, Spain and the UK were calculated using the method proposed in Mackinson and Daskalov (2007). In particular, the proportion of the total catch which is discarded was calculated as follows:

Discards= Catch x Proportion of the catch that is discarded (Dpc)

This can be written as: D = C x Dpc

Equation 13

Similarly,

Landings= Catch x Proportion of the catch that is landed (Lpc)

L=C x Lpc

Equation 14

Or, C= L/Lpc

Equation 15

Substituting equation 15 into equation 13:

Discarded (t) = landed (t) / landed % x discarded %

These formulas were applied to each species for which data of discard rates existed. There is however a limitation in the utilization of this method, in particular the formula

works on the basis that discards can be calculated as a proportion of the landings. This breaks down when 100% of a particular species are discarded, and there are no landings recorded.

Table A3.4 Data derived best estimates for input parameters, with sources summarised. P/B is the Production/biomass ratio over year and it is equivalent to the instantaneous rate of total mortality. Q/B is the Consumption/biomass ratio, where consumption represents the intake of food by a group over year.

	Group name	Biomass (t/km^2)	empirical P/B y^{-1}	empirical Q/B y^{-1}	Landings (t/km^2)	Discards (t/km^2)	References
1	Baleen whales	0.063	0.020	6.323			Hammond and Mackeleod, 2006; Sigurjonsson and Vikingsson, 1997; Trites et al.,1999; Pierce et al., 2004
2	Toothed whales	0.039	0.020	18.595		0.001	Hammond and Mackeleod, 2006; Sigurjonsson and Vikingsson, 1997; Trites et al., 1999; De Pierrepont et al., 2005; Northridge and Mackay, 2004.
3	Seals	0.004	0.060	15.857			Kiely et al., 2000; Bonner, 1994; Trites et al., 1999; Northridge and Mackay, 2004.
4	Seabird offshore-surface feeders	0.001	0.374	98.780			Mitchell et al., 2004; Snow and Perrins, 1998; Votier et al., 2009 unpublished data; Lewis et al., 2001; Thompson et al.,1995; Nelson, 2002; JNCC unpublished data relative to Skomer; Frederiksen et al., 2004; BirdLife International, 2009
5	Seabird inshore-divers	0.00010	0.138	106.100			Mitchell et al., 2004; Snow and Perrins, 1998; Liliendandahl and Solmundsson, 2006; Potts et al., 1980; Frederiksen and Bregnballe, 2000; Birkead et al., 2007; Votier et al., 2005; Votier et al., 2008.
6	Seabird offshore-divers	0.00070	0.062	94.180			Mitchell et al., 2004; Snow and Perrins, 1998; Birkead et al., 2007; Corkhill 1973; Liliendandahl and Solmundsson, 1997; Votier et al., 2005; JNCC unpublished data relative to Skomer; Votier et al., 2008; Votier, unpublished data; Harris and Wanless, 1991; Chapledaine, 1997; Lavers et al., 2008;
7	Gulls	0.0006	0.119	130.150			Mitchell et al., 2004; Snow and Perrins, 1998; Buckley, 1990; Kubetzki and Garthe, 2003
8	Manx shearwater	0.00073	0.141	205.610			Mitchell et al., 2004; Snow and Perrins, 1998; Thompson, 1987; Brooke, 1990
9	European storm petrel	0.000001	0.270				Mitchell et al., 2004; Snow and Perrins, 1998; D`Elbee and Hemery, 1998; Votier et al., 2006
10	Cod	0.425	0.798	3.404	0.049		Cefas ground fish survey 1989-1993, Cefas stomach data base of Pinnegar et al., 2003; ICES data;
11	Juvenile cod		0.872			0.016	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Rochet et al., 2002; Enever et al., 2007
12	Blue whiting	0.444	0.699	6.666	0.003		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
13	Juvenile blue whiting		0.786			0.00006	Cefas stomach data base (Pinnegar et al., 2003); Perez et al., 1996; Enever et al., 2007
14	Hake	0.260	0.903	3.529	0.041		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
15	Juvenile hake		0.895			0.060	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Perez et al., 1996; Enever et al., 2007.
16	Plaice	0.039	1.027	5.131	0.011		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data

Table A3.4 (continued) Data derived best estimates for input parameters, with sources summarised P/B is the Production/biomass ratio over year and it is equivalent to the instantaneous rate of total mortality. Q/B is the Consumption/biomass ratio, where consumption represents the intake of food by a group over year.

	Group name	Biomass (t/km^2)	empirical P/B y^{-1}	empirical Q/B y^{-1}	Landings (t/km^2)	Discards (t/km^2)	References
17	Juvenile plaice		0.834			0.003	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Rochet et al., 2002; Enever et al., 2007
18	Megrim	0.194	0.945	3.820	0.035		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
19	Juvenile megrim		0.790			0.001	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Borges et al., 2005; Rochet et al., 2002; Enever et al. 2007
20	Whiting	0.412	1.055	3.874	0.055		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
21	Juvenile whiting		0.804			0.010	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Rochet et al., 2002; Enever et al., 2007
22	Monkfish	0.290	1.039	2.556	0.057		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
23	Juvenile monkfish		1.084			0.225	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Rochet et al., 2002; Perez et al., 1996; Enever et al., 2007;
24	Haddock	0.159	0.780	4.657	0.008		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
25	Juvenile haddock		0.938			0.008	Cefas stomach data base (Pinnegar et al., 2003); John Casey unpublished data; Enever et al., 2007.
26	Sole	0.053	0.811	5.722	0.004		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data.
27	Mackerel		0.645	1.730	0.069	0.967	Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007.
28	Horse mackerel		0.688	3.510	0.347	0.026	Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007.
29	Red mullet	0.069	0.735	5.962	0.0003		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
30	Sea bass	0.408	0.786	4.407	0.002	0.001	Pawson et al., 2007; Pickett and Pawson, 1994; ICES data; John Casey unpublished data; Enever et al., 2007.
31	Large sharks	0.646	0.819	3.453	0.001		Cefas ground fish survey 1989-1993, Henderson et al., 2000; Joyce et al., 2002; Stanford and Pitcher, 2004; ICES data; John Casey unpublished data.
32	Small sharks	1.521	0.113	4.739			Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003)
33	Pelagic fish	0.046	0.655	7.915	0.089	0.004	Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007.
34	Rays and Skates	0.879	0.387	3.798	0.018		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data

Table A3.4 (continued) Data derived best estimates for input parameters, with sources summarised. P/B is the Production/biomass ratio over year and it is equivalent to the instantaneous rate of total mortality. Q/B is the Consumption/biomass ratio, where consumption represents the intake of food by a group over year.

	Group name	Biomass (t/km^2)	empirical P/B y^{-1}	empirical Q/B y^{-1}	Landings (t/km^2)	Discards (t/km^2)	References
35	Turbot and Brill	0.305	0.592	5.324	0.002		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data;
36	Small and medium flatfish	0.509	0.683	7.767	0.006	0.001	Tidd and Warnes, 2006 Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007
37	Trisopterus spp.	1.890	0.252	7.461	0.003	0.001	Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007.
38	Gurnards	0.406	0.689	5.621	0.002		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data.
39	Pollack and Saithe	3.818	0.787	3.582	0.006		Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data
40	Small benthic fish	0.129	0.475	8.682			Cefas 2mbeam trawl survey; Cefas stomach data base (Pinnegar et al., 2003)
41	Small pelagic spp.	2.550	0.655	9.246			Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003)
42	Garfish		0.676	4.870			Dorman, 1991
43	Demersal predators	0.570	0.779	3.938	0.005	0.001	Cefas ground fish survey 1989-1993, Cefas stomach data base (Pinnegar et al., 2003); ICES data; John Casey unpublished data; Enever et al., 2007.
44	Small crabs and other decapods	0.879	0.950	6.332	0.007	0.002	Cefas 2mbeam trawl survey; Brey, 2002; Stanford and Pitcher, 2004; Christensen, 1995; ICES data; John Casey unpublished data; Enever et al., 2007.
45	Large crabs and lobsters	0.393	0.381	2.540	0.002		Cefas CW COBAS survey; Brey, 2002; Stanford and Pitcher, 2004; Christensen, 1995; ICES data John Casey unpublished data.
46	Small crustaceans	0.560	3.456	23.040			Cefas 2mbeam trawl survey; Brey, 2002; Stanford and Pitcher, 2004; Christensen, 1995
47	Bivalves	25.320	1.104	12.266	0.013	0.006	Cefas 2mbeam trawl survey; Brey, 2002; Stanford and Pitcher, 2004 ICES data; John Casey unpublished data; Enever et al., 2007.
48	Gastropods	1.765	0.655	4.367			Cefas CW COBAS survey; Brey, 2002; Younge, 1946; Christensen, 1995
49	Cuttlefish	0.187	3.000	15.000	0.049	0.002	Cefas CW COBAS survey; Stanford and Pitcher 2004; Mackinson and Daskalov, 2007; Alves et al., 2006; Pauly and Christensen, 1995; ICES data; John Casey unpublished data; Enever et al., 2007.
50	Squid		3.000	15.000	0.017	0.001	Okey and Pauly, 1999; Pierce et al., 1994; ICES data; John Casey unpublished data; Enever et al., 2007.
51	Sessile invertebrate	3.811	0.645	2.580			Cefas CW COBAS survey; Brey, 2002; Stanford and Pitcher, 2004; Haggan and Pitcher, 2005 (based on Morrisette et al., 2003).

Table A3.4 (continued) Data derived best estimates for input parameters, with sources summarised. P/B is the Production/biomass ratio over year and it is equivalent to the instantaneous rate of total mortality. Q/B is the Consumption/biomass ratio, where consumption represents the intake of food by a group over year.

	Group name	Biomass (t/km^2)	empirical P/B y^{-1}	empirical Q/B y^{-1}	Landings (t/km^2)	Discards (t/km^2)	References
52	Echinoderms	7.459	1.376	5.504			Cefas CW COBAS survey; Brey, 2002; Stanford and Pitcher, 2004; Haggan and Pitcher, 2005 (based on Morrisette et al., 2003).
53	Polychaetes	20.815	1.963	13.088			Cefas CW COBAS survey; Brey, 2002; Christensen, 1995; Stanford and Pitcher, 2004
54	Nematoda	0.063	2.500	16.667			Vanaverbeke et al., 1997; Kennedy, 1994; Stanford and Pitcher 2004; Mackinson and Daskalov 2007
55	Zooplankton	19.772	18.000	60.000			Sahfos CPR dataset; Stanford and Pitcher, 2004
56	Carnivorous macroplankton	0.642	7.000	23.330			Conway and Williams, 1986; Weisse and Gomoiu, 2000; Cauffope and Heymans, 2005; Stanford and Pitcher 2004
57	Euphausiids	9.684		23.631			Joint and Williams, 1985; Cauffope and Heymans, 2005; Lasker, 1966; Mackinson and Daskalov, 2007
58	Microflagellate	2.720	200.000	400.000			Joint and Pipe, 1984; Joint and Williams, 1985; Cauffope and Heymans, 2005
59	Pelagic bacteria	0.879	137.118	319.941			Williams, 1981; Joint and Williams, 1985; Mathews and Heimdal, 1980
60	Benthic bacteria	3.247	2.783	247.284			Pfannkuche, 1993; Poremba and Hoppe, 1995; Mathews and Heimdal, 1980; Van Duyl et al., 1993
61	Phytoplankton	40.477	41.511				Joint et al., 2001; Strickland, 1960; Joint and Pomroy, 1987; Pauly and Christensen, 1995
62	Particulate organic matter	56.850					Joint and Williams, 1985; Arias Gonzales, 1994
63	Discards	1.395					Rochet et al., 2002; Borges et al., 2005; Perez et al., 1996; John Casey personal comments
64	Dissolved organic matter	268.837					Cauffope and Heymans, 2005

Table A3.5 Diet matrix showing input values

Prey \ Predator	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. Baleen whales												
2. Toothed whales												
3. Seals												
4. Seabird offshore-surface feeders												
5. Seabird inshore-divers							0.0005					
6. Seabird offshore-divers							0.0827					
7. Gulls							0.0008					
8. Manx shearwater												
9. European storm petrel												
10. Cod					0.0371							
11. Juvenile cod			0.0330		0.0001	0.0026						
12. Blue whiting			0.0010							0.1020	0.0170	
13. Juvenile blue whiting					0.0001	0.0026						
14. Hake												
15. Juvenile hake			0.0340		0.0001	0.0026			0.0149	0.0080		
16. Plaice					0.0342							
17. Juvenile plaice			0.3820							0.0020		
18. Megrim												
19. Juvenile megrim										0.0070	0.0080	
20. Whiting												
21. Juvenile whiting		0.3200	0.1100		0.0001	0.0026				0.0130	0.0020	
22. Monkfish												
23. Juvenile monkfish										0.0120		
24. Haddock												
25. Juvenile haddock			0.0120			0.0026				0.0100		
26. Sole			0.0060							0.0160	0.0080	
27. Mackerel	0.0140	0.3000		0.1360						0.0300	0.0350	
28. Horse mackerel		0.2900	0.0220							0.0540	0.0090	
29. Red mullet												
30. Sea bass												
31. Large sharks												
32. Small sharks										0.0005		
33. Pelagic fish	0.9860	0.0100	0.0002	0.0603	0.4207	0.6419	0.0016	0.3100	0.0030	0.0390	0.0210	0.1550

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
34. Rays and Skates												
35. Turbot and Brill			0.0010							0.0010		
36. Small and medium flatfish			0.0200		0.0019					0.0680	0.0240	
37. Trisopterus spp.	0.0002	0.0700	0.1420	0.0039					0.0927	0.3190	0.2570	
38. Gurnards										0.0001		
39. Pollack and Saithe			0.0360		0.1136							
40. Small benthic fish		0.0100	0.1040	0.0007	0.3634				0.0717	0.2160	0.0720	
41. Small pelagic spp.			0.0250							0.0120	0.0190	
42. Garfish				0.1360					0.0030			
43. Demersal predators			0.0180	0.0050	0.0084					0.0040	0.0080	
44. Small crabs and other decapods				0.0092	0.0111		0.0764	0.0293		0.0550	0.4880	0.1500
45. Large crabs and lobsters					0.0015					0.0270		
46. Small crustaceans				0.0200			0.0424		0.1970		0.0005	
47. Bivalves							0.0437			0.0003	0.0020	
48. Gastropods							0.0004			0.0003	0.0040	
49. Cuttlefish										0.0005	0.0050	
50. Squid			0.0540	0.0032				0.3180		0.0003	0.0010	
51. Sessile invertebrate										0.0005	0.0010	
52. Echinoderms											0.0009	
53. Polychaetes				0.0002			0.0038			0.0040		
54. Nematoda												
55. Zooplankton				0.0035					0.0329			
56. Carnivorous macroplankton									0.0060			
57. Euphausiids						0.0028			0.0149		0.0006	0.6950
58. Microflagellate												
59. Pelagic bacteria												
60. Benthic bacteria												
61. Phytoplankton											0.0180	
62. Particulate organic matter												
63. Discards				0.1450			0.5135					
64. Dissolved organic matter												
65. Import				0.4760	0.0076	0.3425	0.2342	0.3420	0.5640			
Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.
1. Baleen whales												
2. Toothed whales												
3. Seals												
4. Seabird offshore-surface feeders												
5. Seabird inshore-divers												
6. Seabird offshore-divers												
7. Gulls												
8. Manx shearwater												
9. European storm petrel												
10. Cod												
11. Juvenile cod												
12. Blue whiting		0.2510	0.5570			0.1970	0.1390	0.0680				0.0070
13. Juvenile blue whiting												0.0070
14. Hake												
15. Juvenile hake		0.0090	0.0040			0.0080		0.0008		0.0160		
16. Plaice												
17. Juvenile plaice				0.0010								
18. Megrim												
19. Juvenile megrim		0.0030	0.0007			0.0010	0.0160			0.0480	0.0460	
20. Whiting												
21. Juvenile whiting		0.0380						0.0030		0.0090	0.0490	
22. Monkfish												
23. Juvenile monkfish												
24. Haddock												
25. Juvenile haddock						0.0005						
26. Sole								0.0003				
27. Mackerel		0.2030	0.0740			0.0260	0.0130	0.0590		0.4580		0.1970
28. Horse mackerel		0.2010	0.0630			0.1420	0.1060	0.1150		0.1530		0.1850
29. Red mullet												
30. Sea bass												
31. Large sharks												
32. Small sharks		0.0060				0.0060		0.0120				0.0040
33. Pelagic fish		0.1000	0.0890			0.0900	0.0430	0.2120	0.4410			0.1380

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.
34. Rays and Skates												
35. Turbot and Brill												
36. Small and medium flatfish		0.0010	0.0001			0.0030	0.0050	0.0030		0.0970	0.3810	
37. Trisopterus spp.		0.1360	0.1590			0.4050	0.0330	0.3910	0.1500	0.0380	0.1770	0.2750
38. Gurnards		0.0060										
39. Pollack and Saithe												
40. Small benthic fish		0.0010	0.0010			0.0180	0.0530	0.0009	0.0020	0.0020	0.2390	0.0001
41. Small pelagic spp.	0.0090	0.0350	0.0100			0.0490	0.0090	0.0530	0.0020	0.0070	0.0400	0.0900
42. Garfish												
43. Demersal predators		0.0050										
44. Small crabs and other decapods	0.0960	0.0030	0.0160		0.1500	0.0280	0.2670	0.0760	0.1490	0.0220	0.0190	0.0280
45. Large crabs and lobsters		0.0020				0.0050	0.0450	0.0030	0.0008	0.0460		0.0110
46. Small crustaceans			0.0001	0.0170	0.0500		0.0002	0.0001	0.0010			0.0050
47. Bivalves						0.0004	0.0040					0.0050
48. Gastropods						0.0003			0.0050	0.0070		0.0050
49. Cuttlefish			0.0020			0.0040	0.0430	0.0020	0.0490	0.0760		
50. Squid			0.0009			0.0030	0.0170	0.0020	0.0070	0.0220	0.0420	0.0020
51. Sessile invertebrate						0.0010						0.0030
52. Echinoderms			0.0004									0.0270
53. Polychaetes				0.7630	0.2100	0.0005		0.0005				0.0080
54. Nematoda						0.0020			0.0030		0.0080	0.0003
55. Zooplankton					0.1600		0.0003					
56. Carnivorous macroplankton					0.3300							
57. Euphausiids	0.8950		0.0230	0.2190		0.0110	0.2060	0.0003	0.1850			0.0040
58. Microflagellate												
59. Pelagic bacteria												
60. Benthic bacteria												
61. Phytoplankton			0.0001		0.1000		0.0020		0.0070			
62. Particulate organic matter												
63. Discards												
64. Dissolved organic matter												
65. Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.
1. Baleen whales												
2. Toothed whales												
3. Seals												
4. Seabird offshore-surface feeders												
5. Seabird inshore-divers												
6. Seabird offshore-divers												
7. Gulls												
8. Manx shearwater												
9. European storm petrel												
10. Cod												
11. Juvenile cod												
12. Blue whiting			0.0010					0.0090				
13. Juvenile blue whiting			0.0040					0.0090				
14. Hake												
15. Juvenile hake								0.0020				
16. Plaice												
17. Juvenile plaice												
18. Megrim												
19. Juvenile megrim										0.0020		
20. Whiting							0.3330					
21. Juvenile whiting								0.0090		0.0120		
22. Monkfish												
23. Juvenile monkfish								0.0010				
24. Haddock												
25. Juvenile haddock												
26. Sole												
27. Mackerel	0.0070		0.0090			0.3950		0.3440		0.0100		
28. Horse mackerel			0.0610					0.0560		0.0180		
29. Red mullet												
30. Sea bass												
31. Large sharks												
32. Small sharks												
33. Pelagic fish			0.0160			0.0610	0.3330	0.0180	0.0400	0.0010		

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.
34. Rays and Skates										0.0030		
35. Turbot and Brill												
36. Small and medium flatfish							0.1670	0.0030				
37. Trisopterus spp.						0.0180		0.0240		0.0030		
38. Gurnards												
39. Pollack and Saithe												
40. Small benthic fishes	0.0005					0.0090	0.1670	0.0030		0.0140	0.0700	0.0160
41. Small pelagic spp.	0.0004		0.0020	0.0050		0.0880		0.0010	0.0190	0.0009		
42. Garfish												
43. Demersal predators												
44. Small crabs and other decapods	0.1670		0.0870	0.0050	0.2740	0.3950		0.1590	0.0040	0.8420	0.3340	0.1440
45. Large crabs and lobsters	0.0290				0.0790			0.0510		0.0130	0.0440	0.0560
46. Small crustaceans	0.0070		0.0040	0.0008	0.0200			0.0002	0.0060	0.0010		0.0030
47. Bivalves	0.1430							0.0030			0.0005	0.1170
48. Gastropods	0.0260		0.0120	0.0100				0.0010	0.0880		0.0110	
49. Cuttlefish	0.0020							0.0410		0.0140		
50. Squid						0.0260		0.0700		0.0050		
51. Sessile invertebrate	0.0180		0.0070					0.0140				0.1500
52. Echinoderms	0.5220	0.3910			0.2410							0.0150
53. Polychaetes		0.6090	0.0007		0.3870	0.0090		0.0280		0.0150	0.0180	0.3960
54. Nematoda	0.0009		0.0010					0.0010				
55. Zooplankton			0.3760	0.2420					0.0160	0.0001	0.0010	0.0010
56. Carnivorous macroplankton			0.0009					0.0005				
57. Euphausiids	0.0020		0.3950	0.7380				0.1520	0.8240	0.0460	0.5200	0.1020
58. Microflagellate												
59. Pelagic bacteria												
60. Benthic bacteria												
61. Phytoplankton	0.0760		0.0200	0.0002					0.0030			
62. Particulate organic matter												
63. Discards												
64. Dissolved organic matter												
65. Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	37.	38.	39.	40.	41.	42.	43.	44.	45.	46.	47.	48
1. Baleen whales												
2. Toothed whales												
3. Seals												
4. Seabird offshore-surface feeders												
5. Seabird inshore-divers												
6. Seabird offshore-divers												
7. Gulls												
8. Manx shearwater												
9. European storm petrel												
10. Cod												
11. Juvenile cod												
12. Blue whiting		0.0040	0.0040				0.0060					
13. Juvenile blue whiting		0.0040	0.0040				0.0060					
14. Hake												
15. Juvenile hake			0.0230									
16. Plaice												
17. Juvenile plaice												
18. Megrim												
19. Juvenile megrim												
20. Whiting												
21. Juvenile whiting							0.0360					
22. Monkfish												
23. Juvenile monkfish												
24. Haddock												
25. Juvenile haddock												
26. Sole												
27. Mackerel			0.2800				0.2180					
28. Horse mackerel			0.0020				0.2850					
29. Red mullet												
30. Sea bass												
31. Large sharks												
32. Small sharks												
33. Pelagic fish			0.3340			0.5110	0.1620					

Table A3.5 (continued) Diet matrix showing input values.

Prey \ Predator	37.	38.	39.	40.	41.	42.	43.	44.	45.	46.	47.	48.
34. Rays and Skates												
35. Turbot and Brill												
36. Small and medium flatfish	0.0570						0.0240					
37. Trisopterus spp.	0.0010	0.0060	0.2660				0.0850					
38. Gurnards							0.0120					
39. Pollack and Saithe												
40. Small benthic fish	0.0260	0.0290	0.0005				0.0160					
41. Small pelagic spp.		0.0070	0.0500				0.0360					
42. Garfish												
43. Demersal predators												
44. Small crabs and other decapods	0.4240	0.6330	0.0020	0.0872			0.0430	0.1800	0.1800			
45. Large crabs and lobsters	0.0160						0.0570					
46. Small crustaceans	0.0090	0.0040		0.0501	0.0150	0.0834						
47. Bivalves		0.0040				0.0129		0.2000	0.2000			
48. Gastropods	0.0090	0.0030				0.2050						
49. Cuttlefish	0.0280	0.0340	0.0140				0.0120					
50. Squid	0.0340		0.0200									
51. Sessile invertebrate												
52. Echinoderms												
53. Polychaetes	0.0520	0.0030		0.3650		0.1870						
54. Nematoda				0.3650								
55. Zooplankton	0.0010	0.0002	0.0002	0.0501	0.8970							
56. Carnivorous macroplankton					0.0300							
57. Euphausiids	0.3420	0.2700	0.0001	0.0826	0.0580		0.0020					
58. Microflagellate												
59. Pelagic bacteria												
60. Benthic bacteria												
61. Phytoplankton											0.5000	
62. Particulate organic matter								0.6200	0.6200	1.0000	0.5000	1.0000
63. Discards												
64. Dissolved organic matter												
65. Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table A3.5 (continued) diet matrix showing input values.

Prey \ Predator	49.	50.	51.	52.	53.	54.	55.	56.	57.	58.	59.	60.
1. Baleen whales												
2. Toothed whales												
3. Seals												
4. Seabird offshore-surface feeders												
5. Seabird inshore-divers												
6. Seabird offshore-divers												
7. Gulls												
8. Manx shearwater												
9. European storm petrel												
10. Cod												
11. Juvenile cod												
12. Blue whiting												
13. Juvenile blue whiting												
14. Hake												
15. Juvenile hake												
16. Plaice												
17. Juvenile plaice												
18. Megrim												
19. Juvenile megrim												
20. Whiting												
21. Juvenile whiting												
22. Monkfish												
23. Juvenile monkfish												
24. Haddock												
25. Juvenile haddock												
26. Sole												
27. Mackerel												
28. Horse mackerel	0.0030											
29. Red mullet												
30. Sea bass												
31. Large sharks												
32. Small sharks												
33. Pelagic fish	0.2700											

Table A3.5 (continued) diet matrix showing input values.

Prey \ Predator	49.	50.	51.	52.	53.	54.	55.	56.	57.	58.	59.	60.
34. Rays and Skates												
35. Turbot and Brill												
36. Small and medium flatfish	0.0740											
37. Trisopterus												
38. Gurnards												
39. Pollack and Saithe												
40. Small benthic fish	0.0370											
41. Small pelagic spp.	0.2690											
42. Garfish												
43. Demersal predators												
44. Small crabs and other decapods	0.0840	0.0040										
45. Large crabs and lobsters												
46. Small crustaceans	0.0850	0.0030										
47. Bivalves	0.0510			0.0500								
48. Gastropods	0.0020											
49. Cuttlefish	0.0625											
50. Squid	0.0625	0.0040										
51. Sessile invertebrate				0.0100								
52. Echinoderms				0.0600								
53. Polychaetes		0.0010		0.1100								
54. Nematoda			0.1000									
55. Zooplankton		0.0180	0.4500				0.0300	1.0000	0.2260			
56. Carnivorous macroplankton									0.0240			
57. Euphausiids		0.9700										
58. Microflagellate												
59. Pelagic bacteria										1.0000		
60. Benthic bacteria					0.3000	0.2000						
61. Phytoplankton			0.1000	0.0500			0.9000		0.5700			
62. Particulate organic matter			0.3500		0.4000	0.7000			0.1800			
63. Discards												
64. Dissolved organic matter				0.7200	0.3000		0.0700				1.0000	1.0000
65. Import												
Sum	1	1	1	1	1	1	1	1	1	1	1	1

Sensitivity analysis

A sensitivity analysis (sensu Majkowski, 1982) routine is included within Ecopath. This routine varies all basic input parameters (P/B, B, EE, and Q/B) in steps from -50% to +50% to check the effect of altering each of these would be on the 'missing' parameters (i.e. on parameter estimated by Ecopath (EE, Biomass, P/B, or Q/B). The output is given as: (Estimated parameter - original parameter) / original parameter.

The sensitivity of estimated parameters to changes in the input parameters of different groups depended on the degree of trophic connection between those groups. Estimated parameters are generally more sensitive to changes in input parameters; the application of this analysis can be used to indicate food web interactions and as such is complimentary and comparable with other approaches used here, such as mixed trophic impacts (MTI).

In Table A3.6 the sensitivity values of selected functional groups are shown. These correspond to increase/decrease of an input parameter (biomass or EE) of 50% in different functional groups.

For instance, changes in biomass and Q/B of gulls induce important changes in estimated EE of seabird offshore divers and seabird inshore divers that can be interpreted as predatory effects. In addition similar sensitive interaction is between seabird surface feeders Q/B and garfish EE.

Variation in seal biomass affects the EE value of juvenile plaice. Changes in biomass of cod affect juvenile monkfish, sole and juvenile haddock, mostly due to competition and predation effects (these species share their main food resources). Predation could be the explanation of the high sensitivity of various dominantly planktivorous FGs, such as phytoplankton and microflagellates, to changes in Zooplankton biomass or Q/B.

Table A3.6 Sensitivity of estimated EE or biomass of selected FGs of 50% change in input biomass or EE of other FGs. Only sensitivities > 30% are shown. FG: functional group; IP: input parameter; EP: Estimated parameter; EE express the fraction of the production that is used in the system.

FG	IP	Sensitive FG	EP	-50%	-40%	-30%	-20%	-10%	10%	20%	30%	40%	50%
Cod	B	Juv monkfish	EE	-0.3	-0.24	-0.18	-0.12	-0.06	0.06	0.12	0.18	0.24	0.3
Small and medium flatfish	B	Sessile invertebrate	EE	-0.31	-0.24	-0.18	-0.12	-0.06	0.06	0.12	0.18	0.24	0.31
Zooplankton	B	Phytoplankton	Q/B	-0.31	-0.25	-0.19	-0.12	-0.06	0.06	0.12	0.19	0.25	0.31
Pollack and Saithe	B	Squid	B	-0.31	-0.25	-0.19	-0.12	-0.06	0.06	0.12	0.19	0.25	0.31
Juv hake	B	Juv blue whiting	EE	-0.34	-0.27	-0.2	-0.13	-0.06	0.06	0.13	0.2	0.27	0.34
Cod	B	Sole	EE	-0.35	-0.28	-0.21	-0.14	-0.07	0.07	0.14	0.21	0.28	0.35
Demersal predators	B	Gurnards	EE	-0.37	-0.3	-0.22	-0.15	-0.07	0.07	0.15	0.22	0.3	0.37
Seals	B	Juv plaice	EE	-0.39	-0.31	-0.23	-0.15	-0.07	0.07	0.15	0.23	0.31	0.39
Small crabs and other	B	Bivalves	EE	-0.39	-0.31	-0.23	-0.15	-0.07	0.07	0.15	0.23	0.31	0.39
Large sharks	B	Whiting	EE	-0.42	-0.34	-0.25	-0.17	-0.08	0.08	0.17	0.25	0.34	0.42
Cod	B	Juv haddock	EE	-0.45	-0.36	-0.27	-0.18	-0.09	0.09	0.18	0.27	0.36	0.45
Nematoda	B	Benthic bacteria	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Zooplankton	B	Microflagellate	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Microflagellate	B	Pelagic bacteria	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Gulls	B	Seabird offshore divers	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Gulls	B	Seabird-inshore divers	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Cod	Q/B	Juv monkfish	EE	-0.3	-0.24	-0.18	-0.12	-0.06	0.06	0.12	0.18	0.24	0.3
Small and medium flatfish	Q/B	Sessile invertebrate	EE	-0.31	-0.24	-0.18	-0.12	-0.06	0.06	0.12	0.18	0.24	0.31
Zooplankton	Q/B	Phytoplankton	Q/B	-0.31	-0.25	-0.19	-0.12	-0.06	0.06	0.12	0.19	0.25	0.31
Pollack and Saithe	Q/B	Squid	B	-0.31	-0.25	-0.19	-0.12	-0.06	0.06	0.12	0.19	0.25	0.31
Juv hake	Q/B	Juv blue whiting	EE	-0.34	-0.27	-0.2	-0.13	-0.06	0.06	0.13	0.2	0.27	0.34
Cod	Q/B	Sole	EE	-0.35	-0.28	-0.21	-0.14	-0.07	0.07	0.14	0.21	0.28	0.35
Demersal predators	Q/B	Gurnards	EE	-0.37	-0.3	-0.22	-0.15	-0.07	0.07	0.15	0.22	0.3	0.37
Seals	Q/B	Juv plaice	EE	-0.39	-0.31	-0.23	-0.15	-0.07	0.07	0.15	0.23	0.31	0.39
Small crabs and other	Q/B	Bivalves	EE	-0.39	-0.31	-0.23	-0.15	-0.07	0.07	0.15	0.23	0.31	0.39
Large sharks	Q/B	Whiting	EE	-0.42	-0.34	-0.25	-0.17	-0.08	0.08	0.17	0.25	0.34	0.42
Cod	Q/B	Juv haddock	EE	-0.45	-0.36	-0.27	-0.18	-0.09	0.09	0.18	0.27	0.36	0.45
Nematoda	Q/B	Benthic bacteria	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Seabird-surface feeders	Q/B	Garfish	B	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Gulls	Q/B	Gulls	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Zooplankton	Q/B	Microflagellate	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Gulls	Q/B	Seabird offshore divers	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5
Gulls	Q/B	Seabird-inshore divers	EE	-0.5	-0.4	-0.3	-0.2	-0.1	0.1	0.2	0.3	0.4	0.5

APPENDIX 4

Evaluation of model dynamics

Testing the model stability

Testing the basic dynamic behavior of the Celtic Sea model was carried by evaluating the stability of the model when moved away from the equilibrium state described by Ecopath. Prior to fitting the model with observation data we tested for possible instabilities: 1) predator-prey cycles and their relation to multi-trophic level patterns; 2) system simplification (loss of biomass pools due to competition/predation effects); 3) stock-recruitment instabilities (Christensen et al., 2005).

A small perturbation in the combined fishery was simulated and the behavior of the functional groups was scrutinized to search for possible unstable behavior of those groups, and also the speed at which equilibrium was re-established was examined. In order to correct the model for instabilities adjustment to Ecosim parameters (e.g. feeding time factors, prey vulnerabilities and adult-juvenile linkages) were made. A small increase in the combined fishery favored some fish groups (i.e. gurnards, trisopterus and small benthic fish) and seabirds (i.e. gulls), while fish top predators (i.e. cod, haddock, monkfish, hake) and seabirds offshore divers were disadvantaged by the increase. All the groups returned to equilibrium around ten years after the cessation of the disturbance (Fig. A4.1a). In absence of fishing, fish top-predators (i.e. cod, monkfish, haddock, and hake) and most of the apex predators (i.e. seabird offshore divers, seabird inshore divers, seals and toothed whales) increase in biomass. Conversely, gulls, seabird offshore-surface feeders and gurnards exhibit a decrease in biomass (Fig. A4.1b).

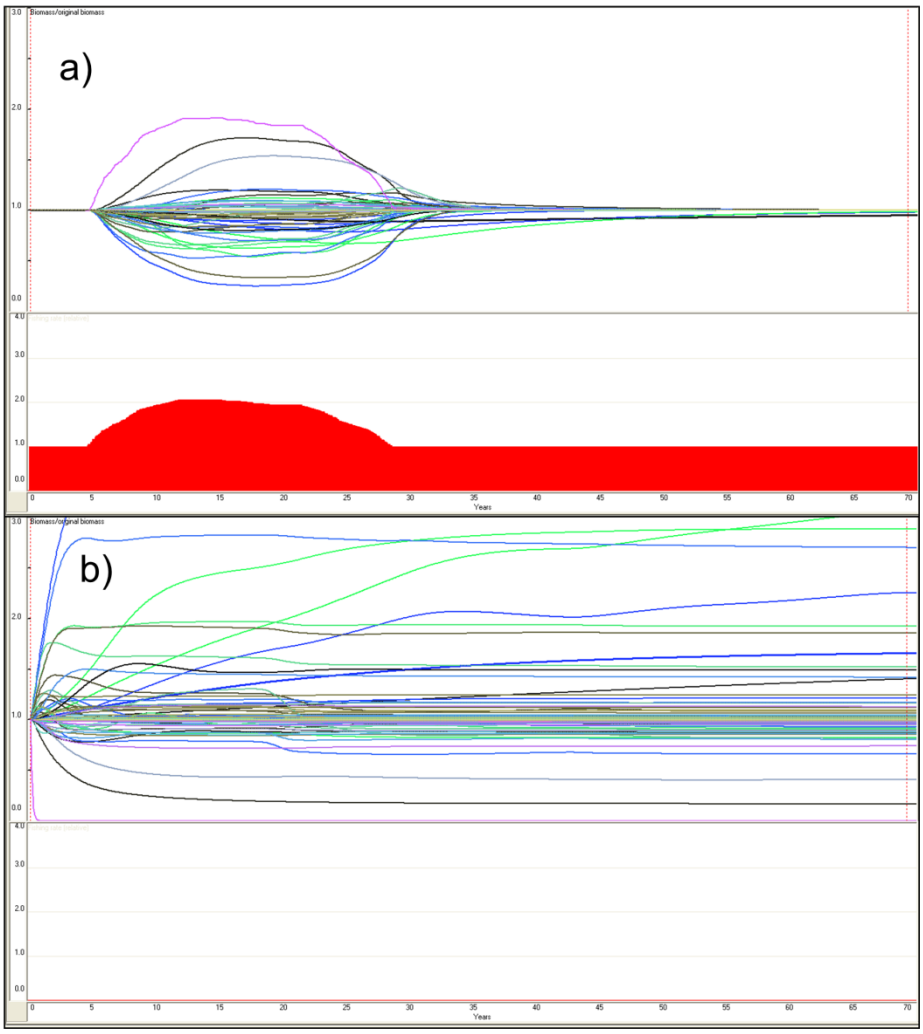

Figure A4.1 (a) Celtic Sea ecosystem response to a small increase in combined fishing effort. The bottom plot shows an increase in fishing effort from the baseline (1.0). The upper plot shows groups that are temporarily disturbed and their subsequent recovery. (b) Ecosystem response to cessation of fishing. Upper plot shows the system response.

Adult-juvenile parameterization

In the Celtic Sea model adult-juvenile parameters for cod (*Gadus morhua*), blue whiting (*Micromesistius poutassou*), hake (*Merluccius merluccius*), plaice (*Pleuronectes platessa*), megrim (*Lepidorhombus whiffiagonis*), whiting (*Merlangius merlangus*), monkfish (*Lophius piscatorius* and *Lophius budegassa*) and haddock (*Melanogrammus aeglefinus*) were set to produce an "emergent" stock-recruitment (SR) relationship comparable to those based on ICES stock assessment and based on Beverton-Holt curves (Beverton and Holt, 1957). To parameterize stock-recruitment relationships fishing was decreased then switched off for ten years, then increased gradually for 25 years. The emergent stock-recruitment relationships were initially erratic and did not resemble those of ICES. Christensen et al. (2000), detail that at least two initial conditions are needed to eliminate stock recruitment instabilities: 1) the juvenile group must have a relatively high P/B rate (total mortality rate) or 2) relatively high EE (so the most mortality is accounted for as predation effects within the model). Both these conditions were satisfied in the model in most cases. In order to produce stock-recruitment relationships adjustments were made to additional parameters (feeding time adjustment rate, and predator effect on feeding time). The result showed that for almost all species was possible to reproduce a stock-recruitment curve, with the exception of blue whiting and plaice were the model showed some minor instability (Fig. A4.2).

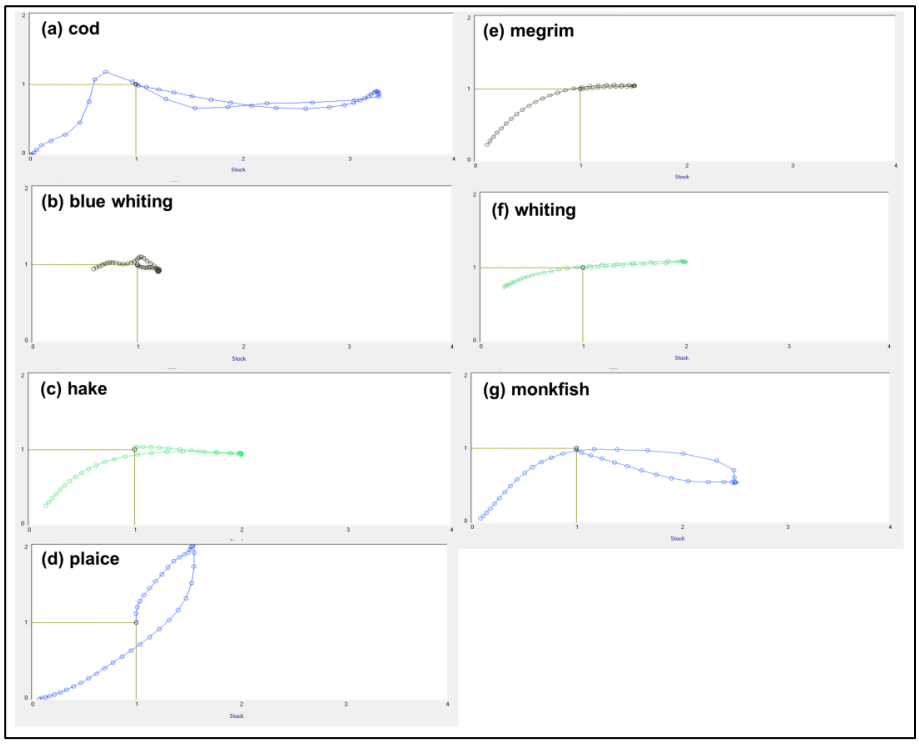

Figure A4.2 Parameterised stock-recruitment curve for some fish species in the Celtic Sea model.

Model sensitivity to vulnerabilities

The effect of different vulnerability estimates on model behavior were examined by creating an increase in fishing effort that persisted for 10 years before decreasing back to the baseline fishing mortality rate (sensu Blanchard et al., 2002). Simulations were run for 70 years. For vulnerabilities in the range of 1.4 (bottom-up) to 4 simulations exhibited persistence of all groups and relative stability (Fig. A4.3). When vulnerabilities were increased beyond 5 the model exhibited erratic behavior. Although all simulation should be carried out under a range of vulnerabilities under a range of setting for all predator-prey pairs, the simple test performed here suggest that vulnerability setting between 1.4 and 4 provides reasonable dynamics and stability.

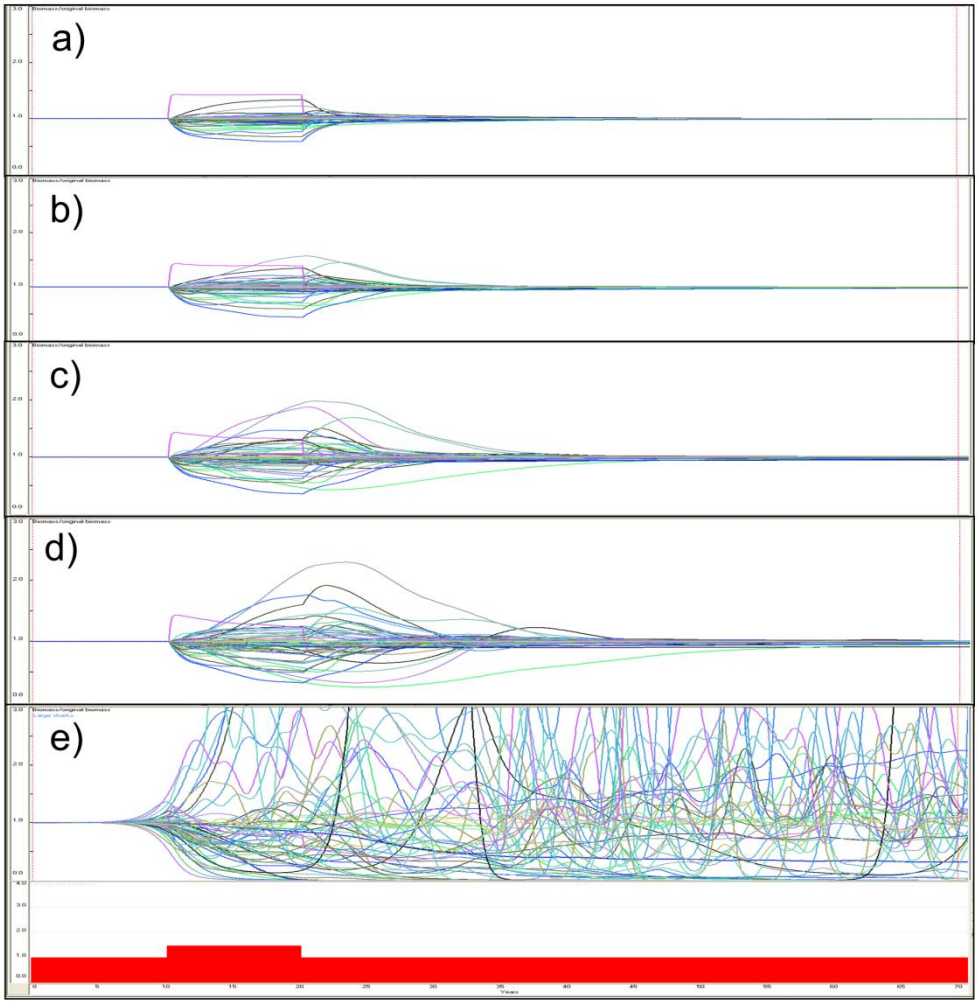

Figure A4.3 Effects on changes in the vulnerability parameter setting on the persistence of functional groups (a) v=1.4; (b) v= 2; (c) v=3; (d) v=4; (e) v=20 (the latter is presented only to show the erratic model behaviour under high vulnerability value setting).

Fitting the Celtic Sea model

In fitting the Celtic Sea model it was assumed that both fisheries and climate variability might have influenced the historical change of species abundance in the ecosystem. The Celtic Sea model was fitted following the step iterative procedure described by Mackinson et al. (2009). The most sensitive interactions between predators and prey were identified by using the sensitivity test routine (Christensen et al., 2005). During the fitting procedure we used the optimisation routine to search for improved estimates of vulnerability (v) for those species that we had time series data for, or which were identified as being particularly sensitive (for more details see Mackinson et al., 2009).

Vulnerability values are estimated in Ecosim during a lengthy iterative procedure that uses optimisation algorithms to improve the goodness of fit between model predictions and observed data by making adjustments to the vulnerability parameters. Vulnerability is the key trophic parameter that is modified in the Sum of Square minimisation procedure. The vulnerability parameter represents the rate of exchange (flow control) of biomass between two prey behavioural states: a state vulnerable to predation and a state invulnerable to predation (see Walters et al., 1997). It determines the strength of interaction between predators and prey and the degree of compensatory changes in recruitment for multistanza groups.

A Marquardt nonlinear search algorithm with trust region modification of the Marquardt steps is used to search for vulnerabilities that improve model fits. For each step in the search, the algorithm runs the Ecosim model at least N+ 1 times, where N is the number of parameters with non-zero variances. The algorithm stops when these changes become very small (or a numerical error occurs in the search calculations) (Christensen et al., 2005). Vulnerabilities for the other groups were left at the default value (Table A4.4).

The model fit for the Celtic Sea is shown in Fig. A4.4 and represents the best overall fit to all groups selected on the basis of the lowest weighted sum of squares differences SS between log reference and log predicted biomass (Christensen et al., 2005).

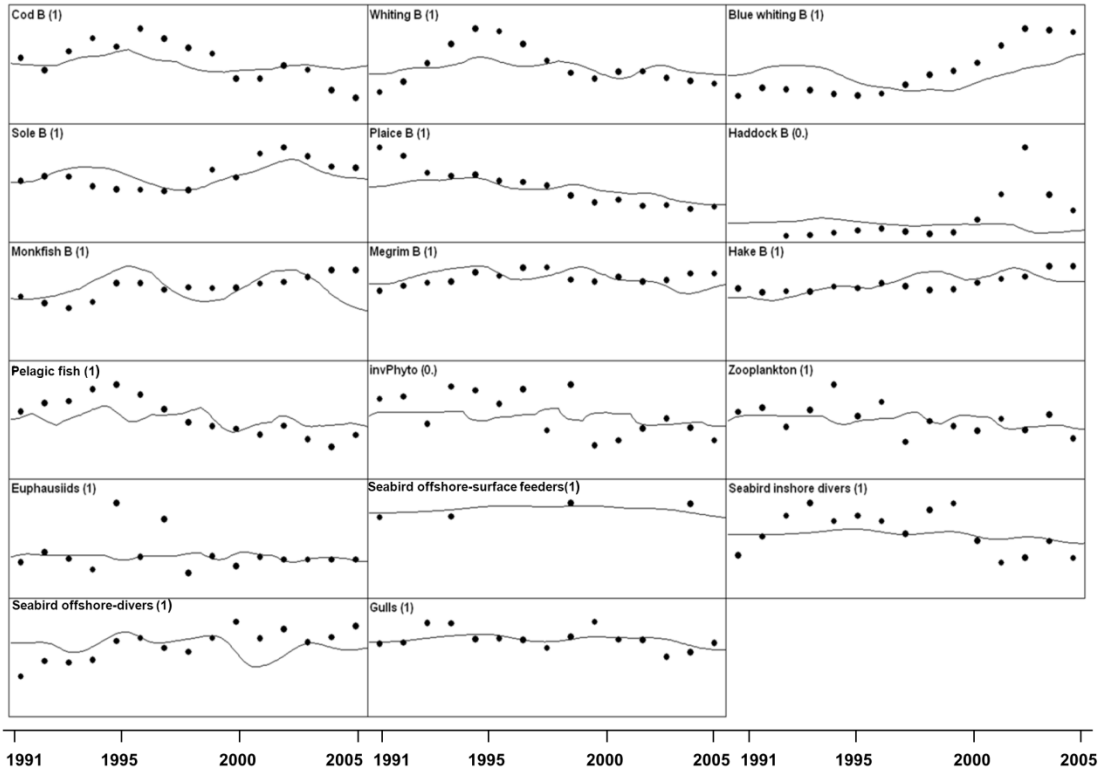

Figure A4.4 Celtic Sea model fit to time series data. Fish data were collected from ICES stock assessment, plankton data from the Continuous Plankton Recorder (SAHFOS), and seabird data from the national Seabird Monitoring Programme database (Joint Nature Conservation Committee, JNCC); more details are given in the material and methods section of the manuscript. Weights applied in the model fitting are also shown: (1) weight applied, (0) weight not applied for that group.

Table A4.1 Time series used in the model fitting.

year	Cod (t)	Whiting (t)	Blue whiting (t)	Sole (t)	Plaice (t)	Haddock (t)	Monkfish (t)	Megrim (t)	Hake (t)	Pelagic fish (herring t)	InvPhyto (cell count)	Zooplankton (mg/m^3)	Euphausiids (mg/m^3)	Offshore Surface Feeders (t)	Inshore Divers (t)	Off-shore Divers (t)	Gulls (t)
1991	10090	24201	2051110	3561	2804		60736	51846	102910	49277	232440.98	8.80	2.35	161.06	1.33	11.64	32.39
1992	8223	32071	2658599	3816	2552		54777	55567	97291	55440	238806.58	9.34	3.03		1.92	16.12	32.85
1993	11091	46192	2542144	3806	2051	13145	49952	57915	99118	56811	160202.21	6.84	2.59		2.56	15.69	41.56
1994	13101	60874	2476177	3235	1962	14620	55575	58751	98324	65516	268025.30	9.04	1.88	162.13	2.96	16.51	41.37
1995	11841	72334	2215170	3063	2002	19057	73688	65577	105559	68768	256531.53	12.34	6.27		2.40	21.93	34.30
1996	14565	70337	2072247	3040	1816	23804	73301	62969	103595	61634	218103.21	8.24	2.72		2.56	22.81	34.63
1997	13078	60755	2227404	2963	1785	28126	67317	68934	110252	51023	260517.43	10.08	5.20		2.40	19.91	34.07
1998	11651	48148	2883554	3019	1677	21456	69337	69124	106421	41577	141372.55	4.89	1.65		2.00	18.79	30.41
1999	10770	38685	3619245	4198	1380	16865	68633	60070	100635	38675	273650.27	7.56	2.76	188.83	2.75	22.82	35.48
2000	6913	34273	3909096	3765	1180	19804	69032	58650	101919	36614	98698.75	6.95	2.12		2.95	27.56	42.09
2001	6900	39494	4521358	5144	1254	45671	72989	62150	111059	32458	112895.62	6.35	2.71		1.79	22.73	34.24
2002	8956	40068	5797550	5495	1072	97212	74440	58770	116462	38846	146477.01	7.90	2.55		1.10	25.48	34.13
2003	8302	34840	7034001	4990	1101	192923	79172	59633	119884	29084	176191.95	6.44	2.55		1.26	21.67	26.54
2004	5128	32526	6935963	4390	983	97010	85653	64712	134930	23736	149270.03	8.46	2.55	187.54	1.77	23.07	28.61
2005	3999	30659	6783310	4308	1057	64763	85653	64712	134930	32302	112329.49	5.33	2.55		1.25	26.34	32.76

Feeding behaviour in Ecosim

In Ecosim predation rates are also assumed to be dependent on how much time organisms spend feeding. In particular, for a functional group, such as hake, increasing the proportion of time spent feeding implies increased vulnerability of prey to hake, and also increased vulnerability of hake to predation.

This is a fundamental link between acquiring food resources and exposure to being a food resource, such that natural selection has acted to "balance" the benefits of increased foraging time against the predation risk costs. The Ecosim vulnerability parameters are in fact assumed proportional to relative feeding time: consumption rate increases proportionally as feeding time increases, but so does vulnerability to predators. In Ecosim it is possible to add information of species feeding behaviour for each functional group in the Group info tab (Christensen et al., 2005). In this study, changes were made to two parameters: feeding time adjustment rate and predator effect on feeding time. The first parameter describes the time that each predator will have to spend feeding (and hence be at a greater risk to predation themselves) when the prey becomes more scarce and varies between 0 and 1 (low values indicating less time spent feeding); while the second parameter describes the risk sensitive foraging behaviour (it varies between 0 and 1; for top or apex predators this value is usually 0).

Feeding time adjustment rate values were set according to these criteria: 0.1 for top-predators (including marine mammals); 0.5 for seabirds; 1 for juvenile fish; 0.5 for piscivorous fish; 0.75 for mackerel and horse mackerel; 0.6 for red mullet; 1 for mid and low trophic levels (including fish, squid and invertebrates) and 0 for plankton and sessile invertebrates (Mackinson and Daskalov, 2007). Predator effect on feeding time values were set according to these criteria: 0 for top predator; 1 for adult fish; 0 for juvenile fish (as they will carry on feeding despite the risk of predation); 0.5 for other groups and benthos (according to Mackinson and Daskalov, 2007).

In some cases minor adjustments were made to these parameters in order to account for potential erratic behaviour in the model. Values used in the model fitting are shown in Table A4.2.

Table A4.2: Group feeding parameters in Ecosim (values used in the fitted model)

	Group	Feeding time adjustment rate	Predator effect on feeding time
1	Baleen whales	0.1	0
2	Toothed whales	0.1	0
3	Seals	0.1	0
4	Seabird offshore-surface feeders	0.5	0
5	Seabird inshore-divers	0.5	0
6	Seabird offshore-divers	0.5	0
7	Gulls	0.5	0
8	Manx shearwater	0.5	0
9	European storm petrel	0.5	0
10	Cod	0.1	0
11	Juvenile cod	1	0
12	Blue whiting	0.8	1
13	Juvenile blue whiting	1	0
14	Hake	0.1	0
15	Juvenile hake	1	0
16	Plaice	0.5	0.3
17	Juvenile plaice	1	0
18	Megrim	0.5	1
19	Juvenile megrim	1	0
20	Whiting	0.5	1
21	Juvenile whiting	1	0
22	Monkfish	0.1	0
23	Juvenile monkfish	1	0
24	Haddock	0.2	1
25	Juvenile haddock	1	0
26	Sole	1	1
27	Mackerel	0.75	1
28	Horse mackerel	0.75	1
29	Red mullet	0.6	1
30	Sea bass	0.2	1
31	Large sharks	0.1	0
32	Small sharks	0.5	1
33	Pelagic fish	0.5	0.5

Table A4.2 (continued): Group feeding parameters in Ecosim (values used in the fitted model)

	Group	Feeding time adjustment rate	Predator effect on feeding time
34	Rays and Skates	0.1	1
35	Turbot and Brill	0.1	1
36	Small and medium flatfish	0.5	1
37	Trisopterus spp.	1	1
38	Gurnards	0.1	0
39	Pollack and Saithe	0.2	0.5
40	Small benthic fishes	1	1
41	Small pelagic spp.	1	1
42	Garfish	0.2	1
43	Demersal predators	0.5	1
44	Small crabs and other decapods	1	0.5
45	Large crabs and lobsters	1	0.5
46	Small crustaceans	1	0.5
47	Bivalves	1	0.5
48	Gastropods	1	0.5
49	Cuttlefish	0	0.5
50	Squid	0	0.5
51	Sessile invertebrate	1	0.5
52	Echinoderms	1	0.5
53	Polychaetes	1	0.5
54	Nematoda	1	0.5
55	Zooplankton	0	0
56	Carnivorous macroplankton	0	0
57	Euphausiids	0	0
58	Microflagellate	0	0
59	Pelagic bacteria	0	0
60	Benthic bacteria	0	0
61	Phytoplankton	0	0
62	Particulate organic matter	----	----
63	Discards	----	----
64	Dissolved organic matter	----	----

Environmental variables used in the model fitting

Correlations between environmental predictors and plankton groups were investigated prior to model fitting (Table A4.3). For each climate predictor long term data from 1991-2005 were collected. Monthly North Atlantic Oscillation index data were downloaded from the University Corporation for Atmospheric Research (UCAR) website, Climate Analysis section http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatmon) and an annual average value (for December-March) calculated.

Atlantic Multidecadal Oscillation data were extracted from the Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/AMO/) and an annual average calculated. Surface Temperature data were derived from satellite images and collated from the POET database (available at http://poet.jpl.nasa.gov) and an average value (for December-March) was estimated. Plankton biomasses (mg/m^3) were collated from the Continuous Plankton Recorder (SAHFOS).

Table A4.3 Correlation analyses (Pearson's coefficient) of environmental parameters and plankton groups were used to help select parameters for time series (1991-2005) fitting. Significant correlations are shown in bold. Significance is indicated as follow: p value <0.001 ***, p value <0.01**, p value <0.05*. WNAO: Winter North Atlantic Oscillation (average December-March); AMO: Atlantic Multidecadal Oscillation; PP: Phytoplankton Color Index; Zoopl: Zooplankton biomass; Euph: Euphausiids biomass; WSST: Winter Sea Surface Temperature (average December-March).

	Year	WNAO	AMO	PP	Zoopl	Euph	WSST
Year	1						
WNAO	-0.144	1					
AMO	**0.781 *****	-0.301	1				
PP	**0.717 ****	-0.478	**0.686 ****	1			
Zoopl	-0.493	0.098	-0.424	-0.151	1		
Euph	-0.175	-0.416	0.014	0.226	**0.758 *****	1	
WSST	**0.697 ****	-0.177	**0.817 *****	**0.476 ****	-0.305	0.007	1

Table A4.4 Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Baleen whales																
2. Toothed whales																
3. Seals																
4. Seabird offshore-surface feeders																
5. Seabird-inshore divers							4									
6. Seabird offshore divers							4									
7. Gulls							4									
8. Manx shearwater																
9. European storm petrel																
10. Cod		2	2		4											
11. Juvenile cod			2		4	4				3.8						
12. Blue whiting			2							3.8	2			4		
13. Juvenile blue whiting					4	4				3.8				4	1.4	
14. Hake			2							3.8						
15. Juvenile hake					4	4			2	3.8				4	1.4	
16. Plaice			2		4											
17. Juvenile plaice										3.8						3.5
18. Megrim																
19. Juvenile megrim										3.8	2			4	1.4	
20. Whiting																
21. Juvenile whiting		2	2		4	4				3.8	2			4		
22. Monkfish		2														
23. Juvenile monkfish		2								3.8						
24. Haddock			2													
25. Juvenile haddock			2			4				3.8						
26. Sole			2							3.8	2					
27. Mackerel	2	2		4						3.8	2			4	1.4	
28. Horse mackerel		2	2							3.8	2			4	1.4	
29. Red mullet																
30. Sea bass										3.8						
31. Large sharks																
32. Small sharks										3.8				4		
33. Pelagic fish	2	2	2	4	4	4	4	2	2	3.8	2	3.5		4	1.4	

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
34. Rays and Skates																
35. Turbot and Brill		2	2							3.8						
36. Small and medium flatfish			2		4					3.8	2			4	1.4	
37. Trisopterus spp.	2	2	2	4					2	3.8	2			4	1.4	
38. Gurnards										3.8				4		
39. Pollack and Saithe			2		4					3.8						
40. Small benthic fishes		2	2	4	4				2	3.8	2			4	1.4	
41. Small pelagic spp.			2							3.8	2			4	1.4	
42. Garfish				4					2							
43. Demersal predators			2	4	4					3.8	2			4		
44. Small crabs and other decapods				4	4		4	2		3.8	2	3.5	1.3	4	1.4	
45. Large crabs and lobsters					4					3.8				4		
46. Small benthic crustacean				4			4		2		2				1.4	3.5
47. Bivalves							4			3.8	2					
48. Gastropods							4			3.8	2					
49. Cuttlefish										3.8	2				1.4	
50. Squid			2	4				2		3.8	2				1.4	
51. Sessile invertebrate										3.8	2					
52. Echinoderms											2				1.4	
53. Polychaetes				4			4			3.8						3.5
54. Nematoda																
55. Zooplankton				4					2							
56. Carnivorous macroplankton									2							
57. Euphausiids						4			2		2	3.5	1.3		1.4	3.5
58. Microflagellate																
59. Pelagic bacteria																
60. Benthic bacteria																
61. Phytoplankton											2				1.4	
62. Particulate organic matter																
63. Discards				4			4									
64. Dissolved organic matter																

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1. Baleen whales																
2. Toothed whales																
3. Seals																
4. Seabird offshore-surface feeders																
5. Seabird-inshore divers																
6. Seabird offshore divers																
7. Gulls																
8. Manx shearwater																
9. European storm petrel																
10. Cod																
11. Juvenile cod																
12. Blue whiting			1.4	1.9							2					2
13. Juvenile blue whiting		2.5		1.9				2			2					2
14. Hake		2.5														
15. Juvenile hake		2.5		1.9		3		2								2
16. Plaice																
17. Juvenile plaice																
18. Megrim							1.5									
19. Juvenile megrim		2.5				3										
20. Whiting															2	
21. Juvenile whiting				1.9		3	1.5									2
22. Monkfish																
23. Juvenile monkfish																2
24. Haddock																
25. Juvenile haddock		2.5														
26. Sole				1.9												
27. Mackerel		2.5	1.4	1.9		3		2	2		2			2	2	2
28. Horse mackerel		2.5	1.4	1.9		3		2			2					2
29. Red mullet																
30. Sea bass														2		
31. Large sharks																
32. Small sharks		2.5		1.9				2								
33. Pelagic fish		2.5	1.4	1.9	2			2			2			2	2	2

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
34. Rays and Skates						3										
35. Turbot and Brill																
36. Small and medium flatfish		2.5	1.4	1.9		3	1.5								2	2
37. Trisopterus spp.		2.5	1.4	1.9	2	3	1.5	2						2		2
38. Gurnards																
39. Pollack and Saithe				1.9		3										
40. Small benthic fishes		2.5	1.4	1.9	2	3	1.5	2	2					2		2
41. Small pelagic spp.		2.5	1.4	1.9	2	3	1.5	2	2		2	1.5		2		2
42. Garfish																
43. Demersal predators																
44. Small crabs and other decapods	1.4	2.5	1.4	1.9	2	3	1.5	2	2		2	1.5	2	2		2
45. Large crabs and lobsters		2.5	1.4	1.9	2	3		2	2				2			
46. Small benthic crustacean	1.4		1.4	1.9	2			2	2		2	1.5	2			2
47. Bivalves		2.5	1.4					2	2							2
48. Gastropods		2.5			2	3		2	2		2	1.5				2
49. Cuttlefish		2.5	1.4	1.9	2	3			2							2
50. Squid		2.5	1.4	1.9	2	3	1.5	2						2		2
51. Sessile invertebrate		2.5						2	2		2					2
52. Echinoderms								2	2	3			2			
53. Polychaetes	1.4	2.5		1.9				2		3	2		2	2		2
54. Nematoda		2.5			2		1.5	2	2		2					2
55. Zooplankton	1.4		1.4								2	1.5				
56. Carnivorous macroplankton	1.4										2					2
57. Euphausiids		2.5	1.4	1.9	2			2	2		2	1.5				2
58. Microflagellate																
59. Pelagic bacteria																
60. Benthic bacteria																
61. Phytoplankton	1.4		1.4		2				2		2	1.5				
62. Particulate organic matter																
63. Discards																
64. Dissolved organic matter																

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
1. Baleen whales																
2. Toothed whales																
3. Seals																
4. Seabird offshore-surface feeders																
5. Seabird-inshore divers																
6. Seabird offshore divers																
7. Gulls																
8. Manx shearwater																
9. European storm petrel																
10. Cod																
11. Juvenile cod																
12. Blue whiting						2					2					
13. Juvenile blue whiting						2	2				2					
14. Hake																
15. Juvenile hake																
16. Plaice																
17. Juvenile plaice																
18. Megrim		2														
19. Juvenile megrim																
20. Whiting																
21. Juvenile whiting		2									2					
22. Monkfish																
23. Juvenile monkfish				2												
24. Haddock																
25. Juvenile haddock																
26. Sole																
27. Mackerel		2					2				2					
28. Horse mackerel		2									2					
29. Red mullet		2														
30. Sea bass																
31. Large sharks																
32. Small sharks																
33. Pelagic fish		2					2			2	2					

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
34. Rays and Skates		2														
35. Turbot and Brill																
36. Small and medium flatfish					2.1						2					
37. Trisopterus spp.		2				2					2					
38. Gurnards											2					
39. Pollack and Saithe											2					
40. Small benthic fishes		2	2	2	2.1	2	2				2					
41. Small pelagic spp.	3	2				2					2					
42. Garfish																
43. Demersal predators		2														
44. Small crabs and other decapods	3	2	2	2	2.1	2	2	2			2	2.1	2			
45. Large crabs and lobsters		2	2	2							2					
46. Small benthic crustacean	3	2		2	2.1	2	2	2	2	2						
47. Bivalves			2	2		2				2		2.1	2			
48. Gastropods			2		2.1	2				2						
49. Cuttlefish		2			2.1	2					2					
50. Squid		2			2.1		2									
51. Sessile invertebrate				2												
52. Echinoderms				2												
53. Polychaetes		2	2	2	2.1	2		2		2						
54. Nematoda																
55. Zooplankton	3	2	2	2	2.1	2		2	2							
56. Carnivorous macroplankton	3								2							
57. Euphausiids	3	2	2	2	2.1	2		2	2		2					
58. Microflagellate																
59. Pelagic bacteria																
60. Benthic bacteria																
61. Phytoplankton	3														2	
62. Particulate organic matter												2.1	2	2	2	2
63. Discards																
64. Dissolved organic matter																

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
1. Baleen whales																
2. Toothed whales																
3. Seals																
4. Seabird offshore-surface feeders																
5. Seabird-inshore divers																
6. Seabird offshore divers																
7. Gulls																
8. Manx shearwater																
9. European storm petrel																
10. Cod																
11. Juvenile cod																
12. Blue whiting																
13. Juvenile blue whiting																
14. Hake																
15. Juvenile hake																
16. Plaice																
17. Juvenile plaice																
18. Megrim																
19. Juvenile megrim																
20. Whiting																
21. Juvenile whiting																
22. Monkfish																
23. Juvenile monkfish																
24. Haddock																
25. Juvenile haddock																
26. Sole																
27. Mackerel																
28. Horse mackerel	2															
29. Red mullet																
30. Sea bass																
31. Large sharks																
32. Small sharks																
33. Pelagic fish	2															

Table A4.4 (continued) Vulnerability matrix for the fitted Celtic Sea model.

Prey \ Predator	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
34. Rays and Skates																
35. Turbot and Brill																
36. Small and medium flatfish	2															
37. Trisopterus spp.																
38. Gurnards																
39. Pollack and Saithe																
40. Small benthic fishes	2															
41. Small pelagic spp.	2															
42. Garfish																
43. Demersal predators																
44. Small crabs and other decapods	2	3														
45. Large crabs and lobsters																
46. Small benthic crustacean	2	3														
47. Bivalves	2			2												
48. Gastropods	2															
49. Cuttlefish	2															
50. Squid	2															
51. Sessile invertebrate				2												
52. Echinoderms				2												
53. Polychaetes		3		2												
54. Nematoda			2													
55. Zooplankton		3	2					1.4	1.4							
56. Carnivorous macroplankton									1.4							
57. Euphausiids		3														
58. Microflagellate							1.4									
59. Pelagic bacteria										2						
60. Benthic bacteria					2	2										
61. Phytoplankton			2	2			1.4		1.4							
62. Particulate organic matter			2		2	2			1.4	2						
63. Discards																
64. Dissolved organic matter				2	2		1.4				2	2				

References

Aebischer, N. J., Coulson, J. C. and Colebrook, J. M., 1990. Parallel long-term trends across four marine trophic levels and weather. Nature, 347: 753-755.

Aebischer, N., 1993. Immediate and delayed effects of a gale in late spring on the breeding of the Shag *Phalacrocorax aristotelis*. Ibis, 135: 225-232.

Ainley, D.G. Ford, R.G., Brown, E.D., Suryan, R.M., Iron, D.B., 2003. Prey resources, competition, and geographic structure of kittiwake colonies in prince William Sound. Ecology, 84: 709-723.

Alheit, S.D., and Hagen, E., 1997. Long-term climate forcing of European herring and sardine populations. Fisheries Oceanography, 6: 130-139.

Allen, R.R., 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada, 28: 1573-1581.

Alverson, D.L., Freeberg, M.H., Pope, J.G., Murawsky, S.A.,1994. A global assessment of fisheries bycatch and discards. FAO Fisheries technical Paper n 339. Rome, FAO, pp. 233.

Alves, D.M., Cristo, M., Sendao, J., Borges, T.C., 2006. Diet of cuttlefish *Sepia officinalis* (Cephalopoda: Sepiidae) off the south coast of Portugal (eastern Algarve). Journal of Marine Biological Association, 86: 429-436.

Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O., Black, A., 2011. Global seabird bycatch in longline fisheries. Endangered Species Research, 14: 91-106.

Araujo, J., Mackinson, S., Ellis, J.R., and Hart, P.J.B., 2005. An Ecopath model of the western English Channel ecosystem with an exploration of its dynamic proprieties. Science Series Technical Report n 145, pp. 45.

Arias-Gonzalez, J.E., 1994. Fonctionnement trophique d'un ecosystème récifal: secteur de Tiahura, Ile de Moorea, Polynèsie Française. PhD Thesis. Ecole Pratique des Hautes Etudes (EPHE). Universite de Perpignan: pp. 354.

Arnott, S.A., and Ruxton, G.D., 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Marine Ecology Progress Series, 238: 199-210.

Attrill, M.J., and Power, M., 2002. Climatic influence on a marine fish assemblage. Nature, 417: 275-278.

Attrill, M.J., and Power, M., 2004. Partitioning of temperature resources amongst an estuarines fish assemblage. Estuarine coastal and shelf science, 61: 725-738.

Bakun, A., 2004. Regime shifts. In: Robinson AR, Brink K (eds) The sea, Vol 13. Harvard University Press, Cambridge, MA, pp. 971-1018.

Barrett, R.T., and Krasnov, Y.V., 1996. Recent responses to changes in stocks of prey species by seabirds in the southern Barents Sea. ICES Journal of Marine Science, 53: 713-722.

Beaugrand, G., Ibanez, F., and Reid, P.C., 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. Marine Ecology Progress Series, 200: 93-102.

Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692-1694.

Beaugrand, G., and Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology, 9: 801-817.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Progress in Oceanography, 60: 245-262.

Beaugrand, G., 2005. Monitoring pelagic ecosystems using plankton indicators. ICES Journal of Marine Science, 62: 333-338.

Beaugrand, G., Edwards, M., Brander, K., Luczak, C., and Ibanez, F., 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecology Letters, 11: 1157-1168.

Beaugrand, G., Luczack, C., and Edwards, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. Global change biology, 15: 1970-1803.

Belda, E.J., and Sanchez, A., 2001. Seabird mortality on longline fisheries in the western Mediterranean: factors affecting bycatch and proposed mitigating measures. Biology conservation, 98: 357-363.

Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fishery management? Hydrobiologia, 670: 317-333.

Benvenuti, A., 2001. Foraging behaviour and time allocation of chick-rearing Razorbils *Alca torda* at Graesholmen, central Baltic Sea. The ibis, 143: 402-412.

Beverton, R. J. H., and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations Series II Volume XIX, Ministry of Agriculture, Fisheries and Food, U.K., pp.533.

BirdLife International, 2009. European Community Plan of Action (ECPOA) for reducing incidental catch of seabirds in fisheries. Available at: www.rspb.org.uk/ Images/ shadow _ Community_Plan_of_Action_tcm9-246779.pdf (accessed 6 July 2012).

Birkead, T.R., Hatchewell, B.J., Meade, J., 2007. Skomer Island Guillemot Study, TBR`s report, department of animal and plant sciences, University of Sheffield.

Birkhead, T.R., 1977. The effect of habitat and density on breeding success in the Common guillemot (*Uria aalge*). Journal of Animal Ecology, 46 (3): 751-764.

Blanchard, J.L., Pinnegar, J.K., and Mackinson, S., 2002. Exploring maine mammal-fishery interactions using "Ecopath with Ecosim": modelling the Barents Sea ecosystem. Scientific Ser. Technical Report, Cefas Lowestoft, 117: pp. 52.

Blanchard, J., Dulvy, N.K., Jennings, S., Ellis, J.R., Pinnegar, J.K., Tidd, A., Kell, L.T., 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? ICES Journal of Marine Science, 62: 405-411.

Bonner, N., 1994. Seals and Sea Lions of the World. London: Blandford A Cassel Imprint. pp. 224.

Borges, L., Rogan, E., and Officer, R., 2005. Discarding by the demersal fishery in waters around Ireland. Fishery Research, 76: 1-13.

Bost, C.A., Le Maho, Y., 1993. Seabirds as bio-indicators of changing marine ecosystems: new perspectives. Acta Oecol 14: 463-470.

Brander, K.M., Dickson, R.R., Edwards, M., 2003. Use of Continuous Plankton Recorder information in support of marine management: applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. Progress in Oceanography, 58: 175-191.

Brander, K., 2010. Impacts of climate change and fisheries. Journal of Marine systems, 79: 389-402.

Brey, T., 2002.Population dynamics in benthic invertebrates.A virtual handbook. The virtual Handbook http://www.thomas-brey/science/virtualhandbook.

Brooke, M., 1990. The Manx Shearwater, T. & A. D. Poyser, London.

Bryan, P., Wallace, R.L., Lewison, S., McDonald, L., McDonald, R.K., Kot, C.Y., Rhema, S.K., Bjorkland, K., Finkbeiner, E.M., Helmbrecht, S., Crowder, L.B., 2010. Global patterns of marine turtle bycatch. Conservation Letters, 3: 131-142.

Buckley, N.J., 1990. Diet and feeding ecology of great black backed gulls (*Larus marinus*) at a southern Irish breeding colony. Journal of Zoology, London, 222: 363-373.

Burnham, K.P., Anderson, D.R., 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York.

Burnham, K.P., and Anderson, D.R., 2002. Model selection and multimodel inference: a pratical information. Theoretic Approach. Springer-Verlag.

Cairns, D.K., 1987. Seabirds as indicators of marine food supplies. Biological Oceanography, 5: 261-271.

Cairns, D.K., 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor, 94: 811-824.

Camphuysen, C.J., 2001. Seabirds and fisheries interaction. In: Steele J.H., Thorpe S.A. & Turekian K.K. (eds) Encyclopedia of Ocean Sciences: 2677-2686. Academic Press, London.

Camphuysen, C.J. Heubeck, M., Cox, S.L., Bao, R., Humple, D., Abraham, C., Sandoval, A., 2002. The Prestige oil spill in Spain. Atlantic Seabirds, 4: 131-140.

Carder, K. L., Chen, F. R., Lee, Z. P., Hawes, S. K., Kamykowski, D., 1999. Semianalytic Moderate-Resolution Imaging Spectrometer algorithms for chlorophyll a and absorption with bio-optical domains based on nitrate-depletion temperatures Journal of Geophysical Research Oceans, 104: 5403-5421.

Cardinale, M., Hjelm, J., Casini, M., 2004. Effect of temperature on recruitment success of herring and sprat stocks in the North Atlantic. ICES CM 2004/K:01.

Carscadden, J.E., Montevecchi, W.A., Davoren. G.K., Nakashima, B.S., 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES Journal of Marine Science, 59: 1027-1033.

Casey, J.M., and Myers, R.A., 1998. Near extinction of a large, widely distributed fish. Science, 281: 690-692.

Cauffope, G., and Heymans, S.J.J., 2005. Energy contents and conversion factors for sea lion`s prey. In: Guenette, S., and V. Christensen (editors). Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. Fisheries Centre Research Reports, 13(1): 225-237.

Chapdelaine, G., 1997. Pattern of Recoveries of Banded Razorbills (*Alka torda*) in the Western Atlantic and Survival Rates of Adults and lmmatures. Colonial Waterbirds, 20(1): 47-54.

Christensen, V., Pauly, D., 1992. Ecopath II a software for balancing steady state ecosystem models and calculating network characteristics. Ecological Modelling, 61 (3-4): 169 -185.

Christensen, V., 1995. Ecosystem maturity-towards quantification. Ecological Modelling, 77: 3-32.

Christensen, V., and Pauly, D., 1998. Changes in models of aquatic ecosystems approaching carring capacity. Ecological Applications 8(1): Supplement S104-S109.

Christensen, V., Walters, C., and Pauly, D., 2000. Ecopath with Ecosim: a user guide. October 2000 edition. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia pp. 130.

Christensen, V., and Walters, C.J., 2000. Ecopath with Ecosim: methods, capabilities and limitations. Pp 79-105. In: (D. Pauly and T.J. Pitcher (eds)). Methods for assessing the impact of fisheries on marine ecosystems of the North Atlantic. Fisheries Centre Research Reports 8(2): pp. 195.

Christensen, V., and Walters, C., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172:109-139.

Christensen, V., and Walters, C.J., 2005. Using ecosystem modelling approaches for fishery management: where are we? ICES, CM: M, 19.

Christensen, V., Walters, C.J., and Pauly, D., 2005. Ecopath with Ecosim: a user's guide, Fisheries Centre, University of Bristish Columbia, Vancouver, Canada.

Clarke, E.D., Spear, L.B., McCracken, M.L., Marques, F.F.C., Borchers, D.L., Buckland, S.T., Ainley, D.G., 2003. Validating the use of generalized additive models and at-sea survey to estimate size and temporal trends of seabird populations. Journal of Applied Ecology, 40: 278-292.

Collas, M.D., Engelhard, G.H., Möllmann, C., 2007. Resolving climate impacts on fish stocks. RECLAIM report pp. 18.

Conversi, A., Fonda Umani, T., Peluso, T., Molinero, J.C., Santojanni, A., Edwards, M., 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other european basins. Plos one, 5: 1-15.

Conway, D.V.P., and Williams, R., 1986. Seasonal population structure, vertical distribution and migration of the chaetognath *Sagitta elegans* in the Celtic Sea. Marine Biology, 93: 377-387.

Corkhill, P., 1973. Food and feeding ecology of puffins. Bird study, 20:3, 207-220.

Corten, A., 1999. A proposed mechanism for the Bohuslän herring periods. ICES Journal of Marine Science, 56: 207-220.

Corti, S., Molteni, F., and Palmer, T. N., 1999. Signature of recent climate change in frequencies of natural atmospheric circulation regimes. Nature, 389: 799-802.

Cowx, I. G., 2003. Interactions between Fish and Birds: Implications for Management. Oxford: Fishing News Books, Blackwell Science, pp. 374.

Crespin, L., Harris, M.P., Lebreton, J.D., Frederiksen, M., Wanless, S., 2006. Recruitment to a seabird population depends on environmental factors and on population size. Journal of Animal Ecology, 75: 228-238.

Cronin, M., Duck, C., O Cadhla, O., Nairn, R., Strong, D. O., Keeffe, C., 2003. Harbour seals population assessment in the Republic of Ireland. Irish Wildlife Manuals Series Editor, ISSN 1393-6670, pp. 40

Croxall, J. P., McCann, T. S., Prince, P. A., and Rothery, P., 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Islands, South Orkney Islands, 1976-1987: implications for southern monitoring studies. In Sahrage, D. (ed.), Antarctic Ocean and resource availability, Springer Verlag, Berlin, pp. 516-533.

Croxall, J.P., 2006. Monitoring predator-prey interactions using multiple predator species: the South Georgia experience. In: Boyd, I.L., Wanless, S., Camphuysen, C.J. (Eds.), Top Predators in Marine Ecosystems. Cambridge University Press, Cambridge, pp. 157-176.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagic in upwelling systems: patterns of interactions and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine science, 57: 603-618.

Cury, P. M., Shin, Y. J., Planque, B., Durant, J. M., and others, 2008. Ecosystem oceanography for global change in fisheries. Trends in Ecology and Evolution, 23: 338-346.

Cury, P.M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E. J., Österblom, Michelle Paleczny, M., Piatt, J.F., Rou, J., Shannon, L., Sydeman, W.J., 2011. Global seabird response to forage fish depletion one-third for the birds. Science, 334: 1703-1706.

Cushing, D.H., 1982. Climate and fisheries. Academic Press, London.

D`elbee, J., and Hemery, G., 1998. Diet and foraging behaviour of the British Storm Petrel *Hydrobates pelagicus* in the Bay of Biscay during summer. Ardea, 86: 1-10.

Daskalov, G.M., Grishin, A.N., Rodionov, S., Mihneva, S.V., 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. PNAS 104: 25.

De Pierrepont, J.F., Dubois, B., Desormonts, S., Santos, M.B., and Robin, J.P., 2005. Stomach contents of English Channel cetaceans stranded on the coast of Normandy. Journal of Marine Biological Association, 85: 1539-1546.

Diamond, A.W., and Devlin, C.M., 2003. Seabirds as indicators of changes in marine ecosystems: ecological monitoring on machias seal island. Environmental Monitoring and Assessment, 88: 153-175.

Dierschke, V., Garthe, S., and Markones, N., 2004. Aktionradien Helgoländer Dreizehenmöwen Rissa tridactlya und Trottellummen *Uria aalge* während der Aufzuchtphase. Vogelwelt 125:11-19.

Dorman, J.A., 1991. Investigation into the biology of the garfish, *Belone belone* (L.) in Swedish waters. Journal of fish biology, 39 (1): 59-69.

Drent, R.H., and Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. Ardea, 68: 225-252.

Drinkwater, K.F., and Myers, R.A., 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Canadian Journal of Fisheries and Aquatic Sciences, 44: 1568-73.

Durant, J.M., Anker-Nilssen, T., Stenseth, N.C., 2003.Trophic interactions under climate fluctuations: the Atlantic puffin as an example. Proceedings of the Royal Society of London, Series B: Biological Sciences 270: 1461-1466.

Durant, J.M., Stenseth, N.C., Anker-Nilssen, T., Harris, M.P., Thompson, P.M., Wanless, S., 2004. Marine birds and climate fluctuation in the North Atlantic. In: Marine Ecosystems and Climate Variation: The North Atlantic a Comparative Perspective (eds Stenseth, N.C., Ottersen, G., Hurrell, J.W., Belgrano, A.) pp. 95-108. Oxford University Press, Oxford.

Durant, J.M., Hjermann, O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N., and Stenseth, N.C., 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecology Letters, 8: 952-958.

Durant, J.M., Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33: 271-283.

Durant, J.M., Hjermann, D.O., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J.M., Stenseth, N. C., 2009. Pros and cons of using seabirds as ecological indicators. Climate Research 39: 115-129.

Eaton, D.R., 1983. Scad in the North-East Atlantic. Laboratory Leaflet No. 56. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, UK.

Edwards, M., Reid, P., and Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960-1995). ICES Journal of marine Science, 58: 39-49.

Edwards, M., and Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881-884.

Edwards, M., Johns, D.G., Licandro, P., John, A.W.G., Stevens, D.P., 2006. Ecological status report: results from the CPR survey 2004/2005. SAHFOS Tech Rep 3:1-8

Einoder, L.D., 2009. A review of the use of seabirds as indicator in fisheries and ecosystems management. Fisheries Research, 95: 6-13.

Ellis, H.I., and Gabrielsen, G.W., 2002. Energetics of free-ranging seabirds. In Biology of Marine Birds, pp. 359-407. Ed. By E.A. Schreiber, and J. Burger.CRC Press, Boca Raton, FL.

Ellis, J. R., Lancaster, J. E., Cadman, P. S. and Rogers, S. I., 2002. The marine fauna of the Celtic Sea. In Marine biodiversity in Ireland and Adjacent Waters (ed. J. D. Nunn). Ulster Museum, Belfast, pp. 45-65.

Enever, R., Revill, A., Grant, A., 2007. Discarding in the English Channel, Western approaches, Celtic and Irish seas (ICES buarea VII). Fisheries research 86: 143-152.

Enever, R., Revill, A.S., Grantc, A., 2009. Discarding in the North Sea and on the historical efficacy of gear-based technical measures in reducing discards. Fisheries research, 95: 40-46.

EU, 1979. Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds. Official Journal, L. 103:1.

EU, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal, L. 206:0007-0050.

EU, 2008. Council Directive, 08/56/EEC of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive).

EU COM, 2009. Green Paper-reform of the common fisheries policy. Commission of the European Communities, Brussels, launched April 2009 and open to submit comments by 31 December 2009. COM: pp. 163.

FAO, 2003. Fisheries management 2. The ecosystem approach to fisheries. FAO, Rome pp. 121.

Fauchald, P., Skov, H., Skern-Mauritzen M., Johns, D., Tveraa T., 2011. Wasp-Waist Interactions in the North Sea Ecosystem. PLoS ONE 6(7): e22729. doi:10.1371/journal.pone.0022729

Fowler, C.W., 1999. Management of multi-species fisheries from overfishing to sustainability. ICES Journal of Marine Science, 56: 927-932.

Fox, A.D., Desholm, M., Kahlert, J., K. Christensen, I.B.K., Petersen, 2006. Information needs to support environmental impact assessment of the effects of European marine offshore. Ibis, 148: 129-144.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621-3.

Fraser, H. M., Greenstreet, S. P. R., and Piet, G. J., 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. ICES Journal of Marine Science, 64: 1800-1817.

Frederiksen, M., and Bregnballe, T., 2000. Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. Journal of Animal Ecology, 69: 737-752.

Frederiksen, M., Wanless, S., Rothery, P., Wilson, L.J., 2004a. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwake. Journal of Applied Ecology, 41 (6): 1129-1139.

Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P., Wanless, S., 2004b. Scale-dependent climate signals drive breeding phenology of three seabird species. Global change biology, 10: 1214-1221.

Frederiksen, M., Wright, P.J., Harris, M.P., Mavor, R.A., Heubeck, M., Wanless, S., 2005. Regional patterns of kittiwake Rissa tridactyla breeding success are related to variability in sandeel recruitment. Marine Ecology Progress Series, 300: 201-211.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to top predators: bottom up control of a marine food web across four trophic levels. Journal of Animal Ecology, 75:1259-1268.

Frederiksen, M., Edwards, M., Mavor, A.R., Wanless, S., 2007a. Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. Marine Ecology Progress Series, 350: 137-143.

Frederiksen, M., Furness, R.W., and Wanless, S., 2007b. Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. Marine Ecology Progress Series, 337: 279-286.

Frederiksen, M., Mavor, R.A., and Wanless, S., 2007c. Seabirds as environmental indicators: the advantages of combining data sets. Marine Ecology Progress Series, 352: 205-211.

Frederiksen, M., Jensen, H., Daunt, F., Mavor, R.A., Wanless, S., 2008a. Differential effects of local industrial sand lance fishery on seabird breeding performance. Ecological Applications, 18(3): 701-710.

Frederiksen, M., Daunt, F., Harris, M.P., Wanless S., 2008b. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long lived seabird. Journal of Animal Ecology, 77: 1020-1029.

Froese, R., Stern-Pirlot, A., Winker, H., and Gascuel, D., 2008. Size matters: how single species management can contribute to ecosystem-based fisheries management. Fisheries Research, 92: 231-241.

Fromentin, J., and Planque, B., 1996. Calanus and the environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine ecology Progresses Series, 134: 111-118.

Fulton, E.A., Smith, A.D.M., 2004. Lessons learnt from a comparison of three ecosystem models for Port Phillip Bay, Australia. African Journal of Marine Science, 26: 219-243.

Fulton, E., 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems, 81:171-183.

Furness, R.W., 1982. Competition between fisheries and seabird communities. Advance Marine Biology, 20: 225-307.

Furness, R.W., and Birkhead, T.R., 1984. Seabird colony distributions suggest competition for food supply during the breeding season. Nature, 311: 655-656.

Furness, R.W., Hudson, A.V., Ensor, K., 1988. Interactions between scavenging seabirds and commercial fisheries around the British isles. In: Burger J (ed). Seabirds and other marine vertebrate competition, predation and other interactions. Columbia University Press, Cambridge, pp. 240-268.

Furness, R.W., 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-1983. Ibis, 132: 205-217.

Furness, R.W., Greenstreet, S.P.R., Walsh, P.M., 1996. Spatial and temporal variability in the breeding success of seabirds around the British Isles: evidence for distinct sandeel stocks? In: Hunt GL, Furness RW (eds) Seabird/fish interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report No. 216. International Council for the Exploration of the Sea, Copenhagen, pp. 63-65.

Furness, R.W., and Bryant, D., 1996. Effect of wind on field metabolic rates of breeding Northern Fulmars. Ecology, 77: 1181-1188.

Furness, R.W., and Camphuysen, C.J., 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science, 54: 726-737.

Furness, R.W., 1999. Will reduced discarding help or harm seabird populations? In: Ecosystem Approaches for Fisheries Management, pp. 481-488. Alaska Sea Grant College Program AK-SG-99-01, Fairbanks.

Furness, R.W., and Tasker, M.L., 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance and identification of key areas for sensitive seabirds in the North Sea. Marine ecology Progress Series, 202: 253-264.

Furness, R.W., 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. ICES Journal of Marine Science, 59: 261-269.

Furness, R.W., 2003. Impacts of fisheries on seabirds communities. Scientia Marina, 67 (suppl. 2): 33-45.

Furness, R., 2004. Seabird breeding failures, climate change and wind farms. Scottish Bird News, 74: 18-19.

Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M., and Mehlum, F., 1991. Field and laboratory metabolism and thermoregulation in dovekies (*Alle alle*). Auk 108: 71-78.

Garcia, S.M., de Leiva Moreno, I., 2003. Global overview of marine fisheries. In: Sinclair M, Valdimarsson G (eds) Responsible fisheries in the marine ecosystem. FAO, Rome, & CABI Publishing, Wallingford, UK, pp. 1-24.

Garthe, S., Walter, U., Tasker, M.L., Becker, P.H., Chapdelaine, G., Furness, R.W., 1999. Evaluation of the role of discards in supporting bird populations and their effects on the species composition of seabirds in the North Sea. In: Diets of seabirds and consequences of changes in food supply, pp. 29-41. ICES Cooperative Research Report No. 232. ICES Copenhagen.

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A.G., Wilkinson, S., Crawford, R.J.M., 2008a. A junk-food hypothesis for gannets feeding on fishery waste. Proceedings of the Royal Society: B, 275 (1639): 1149-1156.

Grémillet , D., Lewis, L., Drapeau, L., Van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S., Ryan, P.G., 2008b. Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? Journal of Applied Ecology, 45: 610-621.

Gremillet, D., and Boulinier, T., 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. Marine ecology progresses series, 391: 121-137.

Guldberg, O. H., and Bruno, J. F., 2010. The Impact of Climate Change on the World's Marine Ecosystems. Science, 328: 1523-1528.

Haggan, N., and Pitcher, T., 2005. Ecosystem Simulation models of Scotland`s West coast and sea lochs. Fisheries Centre Research Reports, 13 (4): pp. 67.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D`Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact. Science, 319: 948-952.

Hammond, P.S., and Macleod, K. 2006. Progress report on the SCANS-II project. ASCOBANS Advisory Committee, Finland, pp. 6.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., et al. 2006. The impacts of climate change in coastal marine systems. Ecology letters, 9 (2): 228-241.

Harris, M.P., and Wanless, S., 1991. Population studies and conservation of puffins *Fratercula arctica*. Pages 230-248 in Bird Population Studies: Relevance to Conservation and Management (C.M.Perrins, J-.D. Lebreton and G.M. Hirons. Eds). Oxford University Press, Oxford, UK.

Hatch, S. A., Meyers, P.M., Mulcahy, D.M., and Douglas, D.C., 2000. Seasonal movements and pelagic habitat use of murres and puffins determined by satellite telemetry. Condor, 102(1):145-154.

Henderson, A.C., Flannery, K., and Dunne, J., 2000. Observations on the biology and ecology of the blue shark in the North-east Atlantic. Journal of Fish Biology, 58: 1347-1358.

Henderson, P. A., 2007. Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. Journal of the Marine Biological Association of the United Kingdom, 87: 589-598.

Heymans, J.J., Howell, K.L., Ayers, M., Burrows, M.T., Gordon, J.D.M., Jones, E.G., Neat, F., 2010. Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. ICES Journal of Marine Science. 68, 265-280.

Hilborn, R., 2011. Future directions in ecosystem based fisheries management: a personal prespective. Fisheries Research, 108: 235-239.

Hilton, G.M., Furness, R.W., and Houston, D.C., 2000. A comparative study of digestion in North Atlantic seabirds. Journal of Avian Biology, 31: 36-46.

Holligan, P.M., 1981. Biological Implications of Fronts on the Northwest European Continental Shelf Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences, 302: 1472.

Holligan, P.M., Hams, R.P., Newell, R.C., Harbour, D.S., Head, R.N., Linley, E.A.S., Lucas, M.I., Tranter, P.R.G., Weekley, C.M., 1984.Vertical distribution and

portioning of organic carbon in mixed, frontal and stratified waters of the English Channel. Marine Ecology Progress Series, 14 (11): 1-127.

Hunt, G. L. Jr, and Schneider, D. A., 1987. Scale dependent processes in the physical and biological environment of marine birds. In Croxall, J. P., (ed.), Seabirds: feeding ecology and role in marine ecosystems, Cambridge, University Press, pp. 7-41.

Hunt, G. L., Jr, 1990: The pelagic distribution of marine birds in a heterogeneous environment. Polar Research, 8: 43-54.

Hunt, G.L. Jr, Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research II, 49: 5821-5853.

Hunter, J.R., 1980. The feeding beghavior and ecology of marine fish larvae, p. 287-330. In Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behaviour and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Hurrel, J., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science, 269: 676-679.

Hurrell, J.W., and Deser, C., 2010: North Atlantic climate variability: The role of the North Atlantic Oscillation. Journal of Marine Systems, 79: 231-244.

ICES, 2005. Report of the Working Group on Assessment of Hake, Monk and Megrim (WGHMM). ICES CM 2006/ACFM: 01. pp. 67.

ICES, 2006. Report of the Northern Pelagic and Blue Whiting fisheries Working Group (WGNPBW). ICES CM 2006/ACFM: 34, pp. 294.

ICES, 2006a. Report of the Working Group on Assessment of Southern Shelf Demersal Stocks (WGSSDS). ICES CM 2006/ACFM: 33, pp. 694.

ICES. 2006b. Report of the Working Group on the Assessment of Northern Shelf Demersal Stocks (WGNSDS). ICES CM 2006/ACFM: 30, pp.294.

ICES. 2007. Report of the Working Group for Regional Ecosystem Description (WGRED), 19 - 23 February 2007, ICES Headquarters, Copenhagen. ICES CM 2007/ ACE: 02. pp.153.

ICES. 2008. Celtic Sea and West of Scotland. - In: ICES (ed.) Advice book 5, pp. 12.

ICES. 2010. Report of the Herring Assessment Working Group for the Area South of 62n (HAWG), pp. 688.

IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J.,

Postel, S.L., Running, S.W., 2001. Water in a changing world. Ecology Applied, 11: 1027-1045.

Jennings, S., and Kaiser, M., 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology, 34: 201-352.

Jennings, S., Kaiser, M.J., Reynolds, J.D., 2001. Marine fisheries ecology. Blackwell, Oxford.

JNCC report, 2008. UK Seabirds in 2008. Results from the UK Seabird Monitoring Programme. pp.16.

JNCC, 2012; available at http://jncc.defra.gov.uk/page-2889 [April 2012]

Joint, I., Wollast, R., Chou, L., Batten, S., Elskens, M., Edwards, E., Hirst, A., Burkill, P., Groom, S., Gibb, S., Miller, A., Hydes, D., Dehairs, F., Antia, A., Barlow, R., Rees, A., Pomroy, A., Brockmann, U., Cummings, D., Lampitt, R., Loijens, M., Mantoura, F., Miller, P., Raabe, T., Alvarez-Salgado, X., Stelfox, C., Woolfenden, J., 2001. Pelagic production at the Celtic Sea shelf break. Deep-sea Research, 48: 3049-3081.

Joint, I.R., and Pipe, K.R., 1984. An electron microscope study of a natural population of picoplankton from the Celtic sea. Marine Ecology Progress Series, 20: 113-118.

Joint, I.R., and Williams, R., 1985. Demands of the erbivore community on phytoplankton production in the Celtic Sea in August. Marine Biology, 87: 297-306.

Joint, I.R., and Pomroy, I.R., 1987.Activity of heterotrophic bacteria in the euphotic zone of the Celtic Sea. Marine Ecology Progress Series, 41: 155-165.

Joyce, W.N., Campana, S.E., Natanson, L.J., Kohler, H.L., Pratt, JR., Jenses, C.F., 2002. Analysis of stomach contens of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. Journal of Marine Science, 59: 1263-1269.

Kaiser, M.J., Rogers, S., McCandless, D.T., 1994. Improving quantitative surveys of epibenthis communities using a modified 2m beam trawl. Marine Ecology Progress Series, 106: 131-138.

Karpouzi, V.S., Watson, R., and Pauly, D., 2007. Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. Marine Ecology Progress Series, 343: 87-99.

Kelleher, K., 2005. Discards in the worlds marine fisheries: an update. FAO Fisheries Technical Paper. No. 470. Rome. FAO. 2005, 1-131.

Kennedy, A.D., 1994. Carbon partitioning within meiobenthic nematode communities in the Exe Estuary, UK. Marine Ecology Progress Series, 105: 71-78.

Kiely, O., Lidgard, D., Mckibben, M., Connol, N., Baines, M., 2000. Grey Seals: Status and Monitoring in the Irish and Celtic Seas. Maritime Ireland / Wales INTERREG Report NO.3, pp. 85.

Kirby, R.R., Beaugrand, G., and Lindley, J.A., 2009. Synergistic effects of climate and fishing in a marine ecosystem. Ecosystems, 12: 548-561 DOI: 10.1007/s10021-009-9241-9.

Kitaysky, A. S., and Golubova, E. G., 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. Journal of Animal Ecology, 69: 248-262.

Kitaysky, A.S., Hunt, G.L. Jr, Flint, E.N., Rubega, M.A., Decker, M.B., 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Marine Ecology Progress Series, 206: 283-296.

Kober, K., Webb, A., Win, I., Lewis, M., O'Brien, S., Wilson, L. J., Reid, J. B., 2010. An analysis of the numbers and distribution of seabirds within the British Fishery Limit aimed at identifying areas that qualify as possible marine SPAs. JNCC Report, pp. 431.

Kokko, H., Harris, M.P., and Wanless, S., 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot Uria aalge. Journal of Animal Ecology, 73: 367-376.

Kubetzki, U., and Garthe, S., 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology, 143: 199-207.

Lasker, R., 1966. Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. Journal of Fisheries Research Board of Canada, 23: 1291-1317.

Lauck, T., Clark, C., Mangel, M., Munro, G.R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications, 8: 72-78.

Lavers, J. L., Jones, I. L., Diamond, A. W., Robertson, G. J., 2008. Canadian Journal of Zoology, Volume 86, Number 1, pp. 51-61.

Lees, K., and Mackinson S., 2007. An ecopath model of the Irish Sea: ecosystem properties and sensitivity analysis. Sci. Ser. Technical Report. Cefas Lowestoft, 138: pp. 49.

Lewis, S., Wanless, S., Wright, P.J., Harris, M.P., Bull, J., Elson, D.A., 2001. Diet and breeding performance of black-legged kittiwakes *Rissa tridactyla* at a North Sea colony. Marine Ecology Progress Series, 221: 277-284.

Lewison, R.L., and Crowder, L.B., 2003. Estimating fishery by-catch and effects on a vulnerable seabird population. Ecological Applications, 13:743-753.

Lewison, R. L., Freeman, S. A., and Crowder, L. B., 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecology Letters, 7: 221-231.

Lilliendahl, K., and Solmundson, J., 1997. An estimate of summer food consumption of six seabird species in Iceland. ICES Journal of Marine Science, 54: 624-630.

Lilliendahl, K., and Solmundson, J., 2006. Feeding ecology of sympatric European shags *Phalacrocorax aristotelis* and great cormorants *P. carbo* in Iceland. Marine Biology, 149: 979-990.

Link, J.S., Brodziak, J.K.T., Edwards, S.F., Overholtz, W.,J. Mountain, D., Jossi, J.W., Smith, T.D., Fogarty, M.J., 2002. Marine ecosystem assessment in a fisheries management context. Canadian Journal of Fisheries and Aquatic Sciences, 59:1429-1440, 10.1139/f02-115.

Litzow, M.A., Ciannelli, L., 2007. Oscillating trophic control induces community reorganization in a marine ecosystem. Ecology Letters, 10: 1124-1134.

Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications, 13(Suppl): S3-S7.

Luczac, C., Beaugrand, G., Jaffre, M., Lenoir, S., 2011. Climate change impact on balearic shearwater trough a tropic cascade. Biology Letters, 7: 702-705.

Lukacs, P.M., Thompson, W.L., Kendall, W.L., Gould, W.R., Doherty, P.F., Burnham, K.P., Anderson, D.R., 2007. Concern regarding a call for pluralism of information theory and hypothesis testing. Journal of Applied Ecology, 44: 456-460.

Mackinson, S., and Daskalov, G., 2007. An ecosystem model of the North Sea to support and ecosystem approach to fisheries management: description and parameterisation. Technical Report, Cefas Lowestoft, 142: pp.196.

Mackinson, S., Daskalov, G., Heymans, J.J., Neira, S., Arancibia, H., Zetina-Rejónd, M., Jiange, H., Chenge, H.Q., Coll, M., Arreguin-Sanchezd, F., Keebleg, K., Shannonh, L., 2009. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. Ecological modelling, 220: 2972-2987.

Majkowski, J., 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. In: Theory and management of tropical fisheries. ICLARM Conf. Proc. 9. pp. 149- 165, Ed. by D. Pauly and G. I. Murphy.

Mann, K.H., and Lazier, J.R.N., 1996. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. Blackwell Science Publications, Oxford.

Matich, P., Heithaus, M.R., and Layman, C.A., 2011. Contrasting patterns of individual specialization and trophic coupling in two marine predators. Journal of Animal Ecology, 80: 294-305.

Mattehews, J.B.L., and Heimdal, B.R., 1980. Pelagic productivity and food chains in fjord system. NATO Conference series, Serie 4. Marine Science, 4: 377-398.

Mavor, R.A., Parsons, M., Heubeck, M., Pickerell, G., Schmitt, S. 2003. Seabird numbers and breeding success in Britain and Ireland, 2002. UK Nature Conservation Report No. 27. Joint Nature Conservation Committee, Peterborough.

Mavor, R.A., Parsons, M., Heubeck, M., Schmitt, S., 2005. Seabird numbers and breeding success in Britain and Ireland, 2004. UK Nature Conservation Rep No. 29, Joint Nature Conservation Committee, Peterborough.

MCCIP, 2010. Marine Climate Change Impacts Annual Report Card 2010– 2011. (Eds Baxter JM, Buckley PJ, and Wallace, CJ) Summary Report, MCCIP, Lowestoft, pp. 12.

McGinty, N., Power, A.M., and Johnson, M.P., 2011. Variation among northeast Atlantic regions in the response of zooplankton to climate change: not all areas follow the same path. Journal of Experimental Marine Biology and Ecology, 400: 120-131.

Mitchell, P.I., Newton, S.F., Ratcliffe, N., and Dunn, T.E., 2004. Seabird populations of Britain and Ireland. Edit T & AD Poyser, pages 511.

Mitchell, P.I., 2006. Impacts of Climate Change on Seabirds in Marine Climate Change Impacts Annual Report Card 2006 (Eds. Buckley, P.J, Dye, S.R. and Baxter, J.M), Online Summary Reports, MCCIP, Lowestoft, www.mccip.org.uk

Montevecchi, W.A., Birt, V.L., Cairns, D.K., 1988. Dietary changes of seabirds associated with local fisheries failures. Biological Oceanography, 5: 153-161.

Montevecchi, W. A., and Berutti, A., 1990. Avian indication of pelagic fishery conditions in the southeast and northwest Atlantic. In Acta XX Congressus Ornithologici, Christchurch, New Zealand, pp. 2246-2256.

Montevecchi, W.A., 1993. Birds as indicators of change in marine prey stocks. In: Furness R.W., Greenwood D.J. (eds) Birds as monitors of environmental change. Chapman & Hall, London, pp. 217-266.

Montevecchi, W. A., 2002. Interactions between fisheries and seabirds. In: Schreiber, E.A., Burger, J (eds) Biology of marine birds. CRC Marine Biology Series, CRC Press, FL, pp. 527-556.

Montevecchi, W.A., 2007. Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series, 352: 213-220.

Morrisette, L., Despatie, S.P., Savenkoff, C., Hammill, M.O., Bourdages, H. and Chabot, D. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). Canadian Technical Report of Fisheries and Aquatic Sciences, 2497: pp. 94.

Nelson, B., 2002. The Atlantic Gannett, Fenix books limitated pp. 396.

Northridge, S., and Mackay, A., 2004. Report to Invest in Fish Southwest. Work Package 9. Marine mammals, pp. 19.

Odum, E.P.,1969. The strategy of ecosystem development. Science, 164: 262-270.

Okey, T., and Pauly D. (eds.), 1999. A trophic mass-balance model of Alaska's Prince William Sound ecosystem for the post-spill period 1994-1996. 2nd Edition. Fisheries Centre Research Reports 1999, 7 (4): pp. 137.

Oro, D., Bosh, M., and Ruiz, X., 1995. Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans*. Ibis, 137: 347-349.

Oro, D., and Pradel, R., 2000. Determinants of local recruitment ina growning colony of Audouin`s gull. Journal of Animal Ecology, 69: 1-14.

Oro, D., and Furness, R. W., 2002. Influences of food availability and predation on survival of kittiwakes. Ecology, 83: 2516-2528.

OSPAR. 2000. Quality Status Report 2000 Region II – Greater North Sea. - In: Commission, P. b. O. (ed.), pp. 149.

OSPAR. 2002. Quality Status Report 2000 Region III - Celtic Seas. - In: Commission, P. b. O. (ed.), pp. 116.

Österblom, H. Casini, M., Olsson, O., Bignert, A., 2006. Fish, seabirds and trophic cascades in the Baltic Sea. Marine Ecology Progress Series, 323: 233-238.

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems, DOI: 10.1007/s10021-007-9069-0.

Oswald, S.A., Bearhop, S., Furness, R.W., Huntley, B., Hamer, K.C., 2008. Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas *Catharacta skua*. Journal of Avian Biology Volume 39, Issue 2, pages 163-169.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C., and Stenseth, N.C., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1-14.

Ottersen, G., and Stenseth, N.C., 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnology Oceanography, 46: 1774-1780.

Ottersen. G., Stenseth, N.C., and Hurrell, J.W., 2004a. Climatic fluctuations and marine systems: a general introduction to the ecological effects. In Marine ecosystems and climate variation, Oxford University press, pp. 3-14.

Ottersen, G., Alheit, J., Drinkwater, K., Friedland, K., Hagen, E., Stenseth, N.C., 2004b. The response of fish populations to ocean climate fluctuations. In Marine Ecosystems and climate variation. pp. 231.

Overholtz, W. J., and Link, J. S., 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. ICES Journal of Marine Science, 64: 83-96.

Overland, J.E., Alheit, J., Bakun, A., Hurrell, J.W., Mackas, D.L., Miller, A.J., 2010. Climate controls on marine ecosystems and fish populations. Journal of Marine Systems, 79: 305-315.

Pachauri, R., 2007. Climate Change: Synthesis Report (IPCC Secretariat, Geneva, 2007). Panel on Climate Change. Cambridge University Press, Cambridge, U.K. pp. 996.

Parent, B., 2011. Population dymanics of three small pelagic fishes in the Celtic and Irish Seas: sprat *Sprattus sprattus*, pilchard *Sardina pilachardus* and anchovy *Engraulis encrasicoulus* - Master thesis. pp. 45.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., Reid, J. B., 2008. Seabirds as indicators of the marine environment. ICES Journal of Marine Science, 65: 1520-1526.

Parsons, T. R., 1992. The removal of marine predators by fisheries and the impact of trophic structure. Marine Pollution Bulletin, 25: 51-53.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stock. Journal du Conseil International Exploration de Mer, 39: 175-192.

Pauly, D., Christensen, V., and Sambilay, V., 1990.Some features of fish food consumption estimates used by ecosystem modellers. ICES CM 1990/G: 17, pp. 8.

Pauly, D., and Christensen, V., 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. Torres, F., 1998. Fishing down marine food webs. Science, 279: 860-863.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57(3): 697-706.

Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature, 418: 689-695.

Pauly, D., Watson, R., and Alder, J., 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transaction of the Royal Society, 360: 5-12.

Pawson, M. G., Kupschus, S., and Pickett, G. D. 2007. The status of sea bass (*Dicentrarchus labrax*) stocks around England and Wales, derived using a separable catch-at-age model, and implications for fisheries management. ICES Journal of Marine Science, 64: 346-356.

Pearson, T.H., 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology, 37: 521-552.

Perez, N., Trujillo, V., and Pereida, P., 1996. Discards of the trawl and long line Spanish fleet in Ices subarea VII in 1994. ICES CM/Mini: 8. International Council for the Exploration of the Sea. Copenaghen, Denmark.

Perris, C.M., 1996. Eggs, egg formation and the timing of breeding. Ibis, 138: 2-15.

Pfannkuche, O., 1993. Benthic response to the sedimentation of particulate organic matter at the biotrans station, 47º N 20º W. Deep Sea Research, 40: 135-149.

Phillips, R.A., Thompson, D.R., and Hamer, K.C., 1999. The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. Journal of Applied Ecology, 36: 218-232.

Pianka, E. R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics, 4: 53-74.

Piatt, J.F., and Sydeman, W.J., 2007. Seabirds as indicators of marine ecosystems. Theme section, Marine ecology Progress Series, 352: 199-309.

Pickett, G.D., and Pawson, M.G., 1994. Sea bass biology, exploitation and conservation, chapter 3.Chapman and Hall, Fish and Fisheries Series 12.

Pierce, G.J., Boyle, P.R., Hastie, L.C., Santos, M.B., 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fisheries Research, 21: 149-163.

Pierce, G.J., Santos, M.B., Reid, R.J., Patterson, I.A.P., and Ross, H.M., 2004. Diet of minke whales *Balaenoptera acutorostrata* in Scottish (UK) waters with notes on

strandings of this species in Scotland 1992-2002. Journal of Marine Biological Association, 84: 1241-1244.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Science, 305: 346-347.

Pinaud, D., Cherel, Y., Weimerskirch, H., 2005. Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. Marine Ecology Progress Series, 298: 295-304.

Pingree, R.D., Holligan, P.M., Mardell, G.T., Head, R.N., 1976. The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic sea. Journal of the Marine Biological Association UK, 56: 845-873.

Pinnegar, J.K., Jennings, S., O'Brien, C.M., and Polunin, N.V.C., 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Journal of Applied Ecology, 39: 377-390.

Pinnegar, J.K., Trenkel, V.M., Tidd, A.N., Dawson, W.A., and Du Buit, M.H., 2003. Does diet in Celtic Sea fishes reflect prey availability? Journal of Fish Biology, 63 (supplement A), 197-212.

Pinnegar, J.K., Blanchard, J.L., Mackinson, S., Scott, R., Duplisea, D., 2005. Aggregation and removal of weak-links in food web models: system stability and recovery from disturbance. Ecological modelling, 184: 229-248.

Pitois, S.G., and Fox, C.J., 2006. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. ICES Journal of Marine Science, 63: 785-798.

Plagányi, É.E,, Butterworth, D.S. 2004. A critical look at the potential of Ecopath with Ecosim to assist in pratical fisheries management. African Journal of Marine Science, 26: 261-287.

Plagányi, É., 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. Food and Agriculture Organization, Rome, Italy, pp.108.

Planque, B., and Fromentin, J.M., 1996. Calanus and environment in the eastern North Atlantic. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 101-109.

Planque, B., Fromentin, J.M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., Kifany, S., 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems, 79: 403-417.

Poloczanska, E.S., Cook, R.M., Ruxton, G.D., Wright, P.J., 2004. Fishing vs natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modeling approach. ICES Journal of Marine Science, 61: 788-797.

Polovina, J.J., 1984. Model of a coral reef ecosystem. Part I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs, 3: 1-11.

Poremba, K., and Hoppe, H.G., 1995. Spatial variation of benthic microbial production and hydrolytic enzymatic activity down the continental slope of the Celtic Sea. Marine Ecology Progress Series, 118: 237-245.

Potts, G.R., Coulson, J.C., and Deans, I.R., 1980. Popilation dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne islands, Northumbelrand. Journal of Animal Ecology, vol 49: 465-484.

Priede, G., and Miller, P.I., 2009. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: New analysis reveals orientation to a thermal front. Fisheries Research, 95: 370-372.

R Development Core Team, 2010. R: A language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria.

Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C., Planque, B., 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. Journal of Marine Systems, 79: 427-435.

Raven, J.A., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J. et al., 2005. Ocean acidification due to increasing atmospheric carbon dioxide, Report to The Royal Society, pp. 68.

Read, A.J., 2008. The looming crisis: interactions between marine mammals and fisheries, Journal of Mammalogy, 89 (3): 541-548.

Reid, D.G., Walsh, M., and Turrel., W.R., 2001. Hydrography and mackerel distribution on the shelf edge west of the Norwegian deeps. Fisheries research, 50: 141-150.

Reid, P.C., Edwards, M., Hunt, H., Warner, A. J. 1998. Phytoplankton change in the North Atlantic. Nature, 391: 546.

Rice, J., 1995. Food web theory, marine food webs, and what climate change may do to northern fish populations. In: Beamish, R.J. (Ed.), Climate Change and Northern Fish Populations. Canadian Special Publication in Fisheries and Aquatic Science, vol. 121, pp. 561-568.

Richardson, A.,J., and Shoeman, D., S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science, 305: 1609-1612.

Richardson, A. Walne, A.W., John, A.W.G., Jonas, T.D., Lindley, J.A., Sims, D.W., Stevensa, D., Witt, M., 2006. Using continuous plankton recorder data. - Progress in Oceanography 68: 27-74.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Mo¨llmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570-1583.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. (Eds). 2010. Resolving climate impacts on fish stocks. ICES Cooperative Research Report No. 301. pp. 371.

Riou, S., Gray, C.M., de L. Brooke, M., Quillfeldt, P., Masello, J.F., Perrins, C., Hamer, K.C., 2011. Recent impacts of anthropogenic climate change on a higher marine predator in western Britain. Marine Ecology Progress Series, 422:105-112.

Robb, C. K., Bodtker, K. M., Wright, K., and Lash, J., 2011. Commercial fisheries closures in marine protected areas on Canada's Pacific coast: the exception, not the rule. Marine Policy, 35: 309-316.

Rochet, M.J., Peronnet, I., and Trenkel, V.M., 2002. An analysis of discards from the French trawler fleet in the Celtic Sea. ICES journal of Marine Science, 59: 538-552.

Rogan, E., and Mackey, M., 2007. "Megafauna bycatch in drift nets for albacore tuna (*Thunnus alalunga*) in the NE Atlantic. Fisheries Research, 86(1): 6-14.

Rogers, J.C., 1984. The association between the North Atlantic Oscillation and the Southern Oscillation in the northern hemisphere. Monthly Weather Review, 112: 1999-2015.

Rolland, V., Weimerskirch, H., Barbaud, C., 2010. Relative influence of fisheries and climate on the demography of four albatross species. Global Change Biology, 16: 1910-1922.

Royama, T. 1996. Analytical Populations Dynamics. Chapman & Hall.

Sandvik, H., Coulson, T., and Saether, B.E., 2008. A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. Global Change Biology, 14: 703-713.

Sathyendranath, G., Cota, V., Stuart, H., Maass, T., Platt, 2001. Remote sensing of phytoplankton pigments: A comparison of empirical and theoretical approaches Journal of Remote Sensing, 22: 249-273.

Schneider, D. C., 1990: Seabirds and fronts: a brief overview. Polar Research, 8: 17-21.

Schreiber, E.A., 2001. Climate and weather effects on seabirds. In Schreiber, E.A., Burger, J., (eds). Biology of marine birds. CRC Press, Boca Raton, FL, 179-216.

Schreiber, R. W., and Schreiber, E. A., 1984. Central Pacific seabirds and the El Nino Southern Oscillation: 1982 to 1983 perspectives. Science, 225: 713-716.

Shin Y. J., and Cury, P., 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquatic Living Resources, 14: 65-80.

Sigurjonsson, J., and Vikingsson, G.A., 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science, 22: 271-287.

Snow, D.W. and Perrins, C.M., 1998. The birds of the western Paleartic. Concise edition, vol 1, Oxford University press.

Spear, L., and Ainley, D., 1997. Flight behavior of seabirds in relation to wind direction and wing morphology. Ibis, 139(2): 221-233.

Stanford, R., and Pitcher, T., 2004. Ecosystem simulations of the English Channel: climate and trade off. Fisheries Centre Research Reports 12(3): pp. 103.

Steele, J.H., 1998. Regime shifts in marine ecosystems. Ecology Applied, 8: 33-36.

Stokstad, E., 2006. Global Loss of Biodiversity Harming Ocean Bounty, Science, 314: 745.

Strickland, J.D.H., 1960. Measuring the production of marine phytoplankton. Fishery research Board of Canada. Bulletin n 122.

Suryan, R.M., Irons, D.B., Brown, E.D., Jodice, P.G.R., Roby, D.D., 2006. Site-specific effects on productivity of an upper trophic-level marine predator: bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Progress in Oceanography, 68:303-328.

Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe S., Montevecchi, W.A., 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science, 57: 531-547.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., Williams, S. E., 2004. Extinction risk from climate change. Nature, 427: 145-148.

Thompson, D.R., Furness, R.W., and Lewis, S.A., 1995.Diets and long term changes in $\delta^{15}N$ and $\delta^{13}C$ values in Northern Fulmar *Fulmarus glacialis* from two northeast Atlantic colonies. Marine Ecology Progress Series, 125: 3-11.

Thompson, K.R.,1987. The ecology of Manx shearwater *Puffinus puffinus* on Rhum, west Scotland. PhD thesis University of Glasgow.

Thompson, P., and Ollason, J., 2001. Lagged effects of ocean climate change on fulmar population dynamics. Nature, 413: 417-420.

Thompson, R.C., Olsen, Y., Mitchell, R.P., Davis, A., Rowland, S.J., John, A.W.G., D. McGonigle, D., A.E. Russell, A.E., 2004. Lost at sea: where is all the plastic? Science, 304: p. 838.

Tidd, A.N., and Warnes, S., 2006. Species distributions from English Celtic Sea groundfish surveys, 1992-2003. Sci. Ser. Technical Report, Cefas Lowestoft, 137: pp. 51.

Toresen, R. and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries, 1: 231-256.

Toresen, R., 2001. Spawning stock fluctuations and recruitment variability related to temperature for selected Herring (*Clupea harengus*) stocks in the North Atlantic. Herring. Expectations for a new millennium. - Lowell Wakefield Fisheries Symposium Series, pp. 315-334.

Trenkel, V.M., Pinnegar, J.K., Rochet, M,J., Rackham, B., 2004. Different surveys provide similar pictures of trends in a marine fish community but not of individual fish populations. ICES Journal of Marine Science, 61: 351-362.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M., Pauly, D., 1999. Ecosystem change and decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and the commercial whaling hypotheses. Vancouver Fisheries Centre, University of British Columbia, pp. 106.

Tuck, G.N., Polacheck, T., Bulman, C.M., 2003. Spatio-temporal trends in longline fishing effort in the Southern Ocean and implications for seabird bycatch. Biology Conservation, 114: 1-27.

Ulanovicz, R.E., 1986. Growth and Development: Ecosystems Phenomenology. Springer Verlag: New Yor, pp. 203.

Ulanovicz, RE., and Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses, 5: 7-16.

Van Duyl, F.C., Van Raaphorst, W., Kop, A.J., 1993. Benthic bacterial production and nutrient sediment water exchange in sandy North Sea sediments. Marine Ecology Progress Series, 100: 85-95.

Vanaverbeke, J., Soetaert, K., Heip, C., Vanreusel, A., 1997. The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). Journal of Sea Research, 38: 93-107.

Videau, C., 1987. Primary production and physiological state of phytoplankton at the Ushant tidal front (west coast of Brittany, France). Marine Ecology Progress Series, 35: 141-151.

Voss, R. Dickmann, M., and Schmidt, J., 2009. Feeding ecology of sprat (*Sprattus sprattus*, L.) and sardine (*Sardine pilchardus* W.) larvae in the German Bight, North Sea. - Oecologia 51: 117-138.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A.V., Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I., and Thompson, D.R., 2004a. Changes in fisheries discards rates and seabird communities. Nature, 427: 727-730.

Votier, S.C., Bearhop, S., Ratcliffe, N., Phillips, R.A., Furness, R.W., 2004b. Predation by great skuas at a large Shetland seabird colony. Journal of Applied Ecology, 41: 1117-1128.

Votier, S.C., B.J. Hatchwell, A.P. Beckerman, R.H. McCleery, F.M. Hunter, J. Pellat, M. Trinder, T.R. Birkhead. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. Ecology Letters, 8: 1157-1164.

Votier, S.C., Crane, J.E., Bearhop, S., De Leon, A., McSorley, C.A., Minguez, E., Mitchell, I.P., Parsons, M., Phillips, R.A., Furness, R.W., 2006. Nocturnal foraging by great skuas *Stercorarius skua*: implications for conservation of storm-petrel populations. Journal of Ornithology 147: 405-413.

Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H., Hatchwell, B.J., 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. Journal of Animal Ecology, 77: 974-983.

Votier, S.C., Hatchwell B.J., Mears M., Birkhead T.R., 2009. Changes in the timing of egg-laying of a colonial seabird in relation to population size and environmental conditions. Marine Ecology Progress Series, 393: 225-233.

Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D., and Newton, J., 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. Journal of Applied Ecology, 47: 487-497.

Votier, S.C, Archibald, K., Morgan, G., Morgan, L., 2011. The use of plastic debris as nesting material by a colonial seabird and associated entanglement mortality. Marine Pollution Bulletin, 62: 168-172

Walters, C.J., and Martel, S., 2004. Fisheries ecology and management, Princeton University Press, Princeton, New Jersey.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology, 7: 139-172.

Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Marine Ecology Progress Series, 294: 1-8.

Wanless, S., Frederiksen, M., Daunt, F., Scott, B.F., Harris, M.P., 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long term studies. Progress in Oceanography, 72: 30-38.

Weimerskirch, H., Inchausti, P., Guinet, C., and Barbraud, C., 2003. Trends in birds and seal populations as indicators of a system shift in the Southern Ocean. Antarctica Biology Conservation, 87: 273-275.

Weimerskirch, H., Louzao, M., de Grissac, S., Delord, K., 2012.Changes in wind pattern alter albatross distribution and life history traits. Science, 335: 211-214.

Weisse, T., and Gomoiu, M.T., 2000. Biomass and size structure of scyphomedusa *Aurelia aurita* in the northwestern Black Sea during spring and summer. Oxford University Press.

Williams, R., 1981. Vertical distribution of *Calanus finmarchicus* and *C. helgolandicus* in relation to the development of seasonal thermocline in the Celtic Sea. Marine Biology, 86: 145-149.

Wootton, J.T., 1998. Effects of disturbance on species diversity: a multitrophic perpective. American Naturalist, 152: 803-825.

Worm. B., Lotze, H.K., Hillebrand, H., Sommer, U., 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature, 417: 848-51.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 3: 787-790.

Younge, C.M., 1946. On the habits of *Turritella communis*. Journal of Marine Biological Association, 26: 377-380.